Chapter 1
Common Bean Genetics, Breeding, and Genomics for Adaptation to Biotic Stress Conditions

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Abstract Sustainable Development Goal 2 from the United Nations (Zero Hunger) states that there is a pressing need for increasing food production and quality through sustainable agricultural practices to feed the ever-growing human population. One of the key aspects to achieve a sustainable food production is to control plant pests, diseases and weeds through integrated crop management which mainly aims at

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reducing the widespread use of phytochemicals due to their persistence in the air, soil, water and food, as well as the development of biotic stress such as parasite resistance. Legume crops plants are, after cereals, the main source of food for the world population. These plants provide proteins, carbohydrates, minerals, vitamins, oils, fiber and other compounds of high nutraceutical value and beneficial properties for human health. The common bean (*Phaseolus vulgaris* L.) is the most widely used food legume for direct human consumption, and is present in regional, national and international marketson all continents by small farmers and large producers, with both green pods and dried seeds being marketed. Like other crops, beans need to adapt to changing conditions, in the current conditions of climate change. These conditions are producing new situations of abiotic and biotic stresses (mainly

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pests and diseases).Genetic improvement of the common bean includes the knowledge of its genetic diversity and the genome and gene function in response to the current changing environmental conditions. An important long-term challenge is the knowledge of the gene(s) that control relevant traits such as pest and disease tolerance/resistance that affects the crop yield and food security. New technologies built around the recently released common bean genome sequence that facilitates the arise of genomic resources, but they need the support of phenotypic data. Generating new bean cultivars or genotypes with enhanced resistance to different parasitesand new knowledge on possible innovative control methods are relevant for the improvement of a sustainable productivity of bean and its quality in different agrosystems.

Keywords Breeding · Common bean · Diseases · Genetics · Legumes · Pests · *Phaseolus vulgaris*

1.1 Introduction

1.1.1 Domestication and Distribution

Understanding the effects of domestication on genetic diversity of common bean (*Phaseolus vulgaris* L.) is of great importance, not only for crop evolution but also for possible applications, such as the implementation of appropriate biodiversity conservation strategies, and the use of genetic variability in breeding programs under the effects of the climatic changes. An important and widespread characteristics of plant domestication is the reduction in genetic diversity, during the initial domestication process and also during the adaptive radiation from the domestication centers to other areas. This reduction in biodiversity is usually more intense in self-pollinating species such as the common bean compared to cross-pollinated species (Jarvis and Hodgkin 1999). This reduction is caused by stochastic events (that is, a bottleneck and genetic drift due to a reduction in population size) and by natural selection adaptive processes and by artificial selection (Vigouroux et al. 2002).

Bitocchi et al. (2012, 2013) defended a Mesoamerican origin of the common bean, based on the analysis of the diversity and the population structure within the Mesoamerican gene. Furthermore, these authors suggested that wild beans from northern Peru and Ecuador represent an ancient germplasm that includes a part of the genetic diversity of ancestral populations of common bean. The resequencing of the common bean genome confirmed this hypothesis.

Domestication took place after the formation of the Mesoamerican and Andean genetic pools pools, thereforetheir population structure isclearly manifested in the wild populations and the domesticated varieties (Papa and Gepts 2003; Papa et al. 2005, 2007; Rossi et al. 2009).This subdivision of common bean germplasm has been defined by several authors (Papa et al. 2007; Angioi et al. 2009; Bitocchi et al. 2012, 2013) although the domestication events into each genetic pool group is under discussion. Bitocchi et al. (2013) proposed a single domestication event in each

genetic pool and suggested the Oaxaca Valley in Mesoamerica and southern Bolivia and northern Argentina in the Andean regios as tentative areas of domestication of the common bean.

Each of the two domesticated gene pools of the common bean isadditionally subdivided into several ecogeographic races, with a long history of adaptation to specific environmental conditions: Durango, Jalisco, Mesoamerica, and Guatemala in the Mesoamerican gene pool; and Chile, Nueva Granada, and Peru in the Andean gene pool (Singh et al. 1991; Beebe et al. 2001).

The introduction of some exotic species in new agricultural agrosystems raises relevant questions about adaptation, taking into account the requirements of tolerance to several stresses, as well as competence with other native crops (De Ron et al. 2016). Zeven (1997) reported that no records of common bean earlier than 1543 have been found in European herbariums. The dispersion of the common bean to Europe started from the Iberian Peninsula (Spain and Portugal), where this species was introduced mainly from Central America around 1506 and from the southern Andes after 1532, through sailors and traders (Brücher and Brücher 1976; Debouck and Smartt 1995). The pathways of dissemination of the crop across Europe included introductions from America combined with direct seed exchanges between European and other Mediterranean countries (Papa et al. 2007). The phaseolin protein was used as a marker to explain the worldwide dissemination of common bean (Gepts 1988). A high frequency of phaseolin Andean types (T, C, H, and A) was identified compared to the Mesoamerican ones (S, B, M) (Lioi 1989a, 1989b; Santalla et al. 2002; Logozzo et al. 2007).

As mentioned before, the common bean was originated and domesticated in tropical highlands. This means that abiotic and biotic conditions had an influence on the development of European varieties (Rodiño et al. 2006, 2007). In some cases, bean breeders have had to incorporate tolerances to abiotic stresses from sources outside the primary gene pool of common bean. For example, tepary bean could also provide tolerance to heat or drought, and runner bean, tolerance to low soil fertility (Miklas et al. 2006). In the case of rhizobia symbiotic system, it is possible that migration of the species had not been parallel, so additional efforts are underway to achieve efficient symbiotic genotypes of common bean and rhizobia (Rodiño et al. 2011). As a result of plant-rhizobia coevolution, a spectrum of compatible specific rhizobia is recognized for one or more legume species.

1.1.2 Economic Importance of Common Bean as a Food Resource

With more than 19,500 species and 770 genera, legumes (family Fabaceae or Leguminosae) constitute, after the families Asteraceae and Orchidaceae, the third most abundant angiosperm plants in number of species. Legumes played an important role in the early development of agriculture, were domesticated along with grasses, and

today occupy diverse aquatic and terrestrial environments in nearly every biome on Earth, even the most extreme habitats.

Grain legumes are relevant sources of food for a large part of the world population, providing protein, carbohydrates, minerals, vitamins, oil, fiber and other compounds with nutraceutical value and health-promoting properties (Champ 2002). From a nutritional point of view, the amino acid profile of legume storage proteins reveals low amounts of the essential sulfur-containing amino acids (i.e., methionine and cysteine) and tryptophan, while lysine, another essential amino acid, is quite abundant. Legume proteins complement very well those of cereals, which are normally rich in sulfur amino acids and poor in lysine and threonine. Besides the composition in essential amino acids, the nutritional quality of seed proteins is also largely determined by their digestibility; in fact, amino acids composition only represents the potential nutritional quality of a protein, being their bioavailability critical for the supply of amino acids in the diet (Sparvoli et al. 2015).

Beans are produced and consumed mainly as a dry food legume, due to the high protein content of the grain, but the use of the fresh pod as vegetable (snap bean) is common in many areas. Common bean is highly consumed Africa and Latin America (as the most important source of plant protein), as is relevant also in traditional diets of the Middle East, Europe (Broughton et al. 2003; Casquero et al. 2006) and the USA (Blair and Izquierdo 2012).

The role of bean in human diet is on its protein content and alsoon the functional properties. The consumption of common bean could reduce the risk of some diseases such as obesity, diabetes, cardiovascular diseases and colon, prostate, and breast cancer (Hangen and Bennik 2003; Thompson et al. 2009; Sparvoli et al. 2015).

1.1.3 Growing Importance in the Face of Climate Change and Increasing Population

1.1.3.1 Brief Account on Behavior of Beans Under Thermohydric Stress

The bean crop can grow at different latitudes where mean air temperature varies from 14 to 35 °C. Being originated in the medium to high altitude regions, it is sensitive to heat, whereas day and night temperatures above 30 or 20 °C, respectively, result in significant yield reduction (Beebe et al. 2011). According to Araújo et al. (2015), common bean fromthe Andean area adapts better to cooler climate and high altitude (1400–2800 masl) regions, whereas genotypes of Mesoamerican origin adapt to higher temperatures in low to medium altitude (400–2000 masl) regions.

Extensive areas are almost permanently subjected to the action of thermohydric stress conditions. This is highlighted by the aridity index, calculated according to De Martonne's formula, which frequently varies for temperate areas between 22 and 24 °C (Păltineanu et al. 2005). Stress conditions may increase in the future

due to climate change that is affectingmany countries in the world. These changes, caused by the accumulation of greenhouse gases, mainly lead to higher temperatures, increased water stress and increased frequency of storms, factors that limit the level of agricultural production and its quality.

According to Easterling et al. (2007) increasing the average of annual temperature by less than 2 °C has a positive effect on crops in temperate zones but increasing above this limit can have negative effects on plant metabolism and water regime.

Dawson and Spannagle (2009) estimate that in subtropical areas and mid-latitudes in the northern hemisphere, the climate will become drier. If the temperature increases 2 °C by 2050, the precipitation in these areas will be lower by about 30%. But if the temperature increases by 3 °C during this period, the precipitation will decrease by up to 50%. The precipitations will increase in the northern regions of Europe, Asia and America. In areas with temperate climates, precipitation will be reduced in the spring and summer seasons.

Recent projections reported by CGIAR showed that the area suited for bean in eastern and central Africa could shrink up to 50% by 2050. Affecting mainly lowland areas, heat stress will pose a particularly serious problem for bean crops in Malawi and the Democratic Republic of the Congo (DR Congo), followed by Tanzania, Uganda, and Kenya. Across Latin America, the situation is also dire. Bean production in Nicaragua, Haiti, Brazil, and Honduras, as well as Guatemala and Mexico, would be most impacted (CGIAR 2015).

An experiment conducted by Alves da Silva et al. (2020) showed that the crop season factor significantly influenced the performance of genotypes and the high temperatures observed in the summer crop season drastically reduced the grain yield of the cultivars. Due to the high interaction of genotype versus location and season versus location for grain yield, it was observed that investigated genotypes do not exhibit wide adaptability for high temperature, being necessary to carry out the evaluations and selections in unfavorable environments.

1.1.3.2 Limits of Thermohydric Stress at Bean Plants

In the case of worsening thermohydric stress conditions, it is necessary to know the limits of its negative effects, how plants recognize stressors and what is the answer to acclimatization that allows them to survive a shorter period in these conditions. Soil temperature and humidity, within optimal limits, are the main factors that determine the growth and development of bean plants. Outside the optimal limits, temperature and humidity are stressors, effect of which is accentuated as the differences from the optimal limits increase and the duration of action is longer.

The optimum temperature varies mainly depending on the process, organ and phenophase. Thus, the optimum temperature for bean seed germination varies between 8 and 25 °C (Lin and Markhart 1996); for flowering, between 20 and 25 °C (Angelini 1965); for pod setting between 22 and 25 °C and for photosynthesis the optimum temperature is 25 °C (Fraser and Bidwell 1974).

Temperatures outside these limits have a stress effect. Thus, the temperature of 32 °C determines the reduction of the leaf surface, the length of the roots, the rhythm of the net assimilation and the accumulation of the dry matter (Lin and Markhart 1996). The growth rate of bean plants at this temperature is slower compared to that determined at 25 °C. Similar results were obtained by Udomprasert et al. (1996), who found that exposing the roots and stems to high temperature of 45 °C for 5 h reduced the intensity of the photosynthesis process and the growth process.

Critical temperatures, below 8 °C, have a negative effect on the metabolism of bean plants. Thus, Pardossi et al. (1992), stated that seedlings exposed to a temperature of 3 °C have a slow process of abscisic acid biosynthesis and wither quickly because the stomates remain open for the first 24 h. The turgidity of the leaf cells returns to normal after 30–40 h, with the change in the endogenous concentration of abscisic acid. Also, at critical temperatures, lipids in the mitochondrial membranes of bean plants, which have a higher content of saturated fatty acids, passes to the gel phase, inhibiting the transport of pyruvic acid (Lyons and Raison 1973), which accumulates in the cytoplasm, where it is biodegraded anaerobically to acetic aldehyde and ethyl alcohol. The accumulation of these substances causes the characteristic symptoms of the physiological disorder known as low temperature breakdown.

Chasompongpan et al. (1990) found that exposure of bean plants for 5 min at 42 °C reduced the amount of oxygen produced in photosynthesis by 50–95%, and at 45 °C oxygen production is completely canceled. According to Angelini (1965) the minimum temperature for flowering of bean plants is 15 °C. Increasing the temperature during the day to 32 °C has small effect on the abscission of flower buds and flowers but increasing the temperature during the night to 27 °C has reduced the production of pods and seeds due to the abscission of flower buds, flowers, and small pods. Thermal stress (2 days at 35 °C, 10 h per day), affected the pollen more, compared to the pistil. The critical period for thermal stress is between 6 days before flowering, when it can cause abscission of 82% of pods less than 2 cm long (Monterroso and Wien 1990).

1.1.3.3 Effects of Thermohydric Stress on Bean Plants

During the vegetation period, the plants are subjected to longer or shorter periods with thermo-hydric stress. Boyer (1982) considers that water stress is widespread and is the most important abiotic limiting factor for most plants. The sensitivity of plants to the action of thermohydric stress differs, depending on the species and variety, the level of stress, the rate of change and the phenophase in which it manifests itself. Hsiao (1973) considers that water stress is moderate, if the foliar water potential varies between −1.2 and −1.5 MPa and is severe, when the water potential falls below −1.5 MPa. It causes the appearance in bean plants of numerous morphological, physiological, and biochemical changes, which ultimately lead to a decrease in its yield and quality.

From the synthesis of the research results carried out by Trewavas (2003), it resulted that water stress causes changes in the synthesis process of cell walls, cuticle

thickness, stomatal conductivity, leaf size, stomatal density and phenophase development. Thermohydric stress reduces the leaf area of bean plants, both by reducing the number of pods and by reducing their growth rate.

The water requirements of bean plants are higher during flowering and fertilization. Lack of water during this period can cause abscission of flower buds and flowers. Drought resistance of plants is a genetic characteristic that is determined by many factors. Drought tolerance is a complex quantitative trait controlled by many genes and is one of the most difficult traits to study and characterize (Sayadi Maazou et al. 2016). This is highlighted by the drought index which represents the ratio between the yields obtained on non-irrigated plots and on irrigated ones. The value of this indicator varies depending on the genotype between 0.22 and 0.90.

1.1.3.4 Thermohydric Stress Reception

Both thermal and water stress have a common effect, reducing the water content of the soil, generating conditions of osmotic stress. For this reason, the reception of signals induced by thermohydric stress can be done by protein receptors, mainly located in the root cell plasmalemma (Trewavas and Malho 1997). The change and intracellular pressure are received by proteins that act as osmosensors and have been identified in the bacterium *Synechocystis* spp. and called histidine kinases 33 (Mikami et al. 2002). A similar receptor was later identified in *Arabidopsis thaliana*, that was named ATHK1, which is also a histidine kinase (Scheel and Wasternack 2004). The decrease in intracellular pressure changes the configuration of the osmosensor and activates its cytoplasmic component, which acts as a kinase.

The transmission of signals induced by osmotic stress is performed after Lata et al. (2015) with the participation of MAP-kinases (mitogen activated protein kinase), which is the main way of transmitting signals induced by osmotic stress. The transmission of signals can also be achieved with the help of a family of protein kinases (CDPKs) are serine threonine protein kinase Ca^{2+}-dependent protein kinases that have a molecule of calmodulin to the terminal carbon, to which calcium binds. By binding calcium ions to calmodulin, a conformational change occurs that activates the kinase by phosphorylation. The transmission of signals through the protein kinase chain is achieved by successive phosphorylation and dephosphorylation of protein kinases, which finally activate, by phosphorylation, specific transcription factors.

Transcription factors are proteins that activate in the cytoplasm or nucleus and have three structural domains: a binding domain to the gene encoding the response, a transcriptional activating domain, and a ligand binding domain. Transcription factors bind to the cis-regulatory sequence of DNA and activate the transcription process that results in a specific mRNA, which encodes the synthesis of proteins involved in acclimatization reactions to thermohydric stress. Seki et al. (2003) monitored the expression of 7,000 genes induced by drought, salinity and low temperatures and specified that in the case of drought stress occurs the expression of 277 genes and the repression of another 79 genes.

According to Konzen et al. (2019) PvDREB genes are involved in tolerance to abiotic stress, and Soltani et al. (2019) mention that the HSP21, ABA4 and KHCB4.3 genes provide protection of photosystem II to the action of water stress.

The acclimatization process determines the increase tolerance of the plants to the subsequent exposure to more severe thermohydric stress conditions. Key et al. (1981) and Jenks and Hasegawa (2005) found that acclimatization reactions to heat stress are triggered when the ambient temperature is 5–10 °C higher than the optimal value for plant growth. Lin et al. (1984) obtained similar results and found that acclimatization to thermal stress can be achieved by exposing plants to low thermal shock. This led to changes in gene expression and synthesis of heat shock proteins, which prevented the denaturation of cellular proteins under the action of temperatures of 45 °C. The reactions of plants to the action of these stressors are particularly complex. On one hand, stressors stimulate some processes (as free radical synthesis) and on the other, inhibit other processes (as photosynthesis). At the same time, it determines the performance of passive protective reactions, such as the passive closing of the stomata, the change of the position of the leaves in relation to the solar radiation, the withering, etc.

Exposure, a short period of time of bean plants to temperatures and humidity with stress effect, determines their acclimatization, which consists in achieving active changes, genetically coordinated, through which plants exhibit tolerance to stressors, changes that are not transmitted to offspring. The specific receptors, the signal transmission chain, the transcription factors, and the specific genes involved in carrying out these reactions participate in the acclimatization reactions.

1.1.3.5 Synthesis of Abscisic Acid

Thermohydric stress is a signal for specific receptors involved in the synthesis of abscisic acid: histidine kinases HIK33 or AtHK1 that function as osmosensors. Their activation under conditions of osmotic stress, by phosphorylation, the transmission of stress signals through the cascade of phosphorylations and successive dephosphorylation of MAP-kinases and the activation of transcription factors such as ABF1 and AREB2/ABF4 activate genes encoding the enzymes involved in the synthesis of abscisic acid.

Abscisic acid is transported quickly to the leaves, but can also be synthesized at their level, where it causes the opening of calcium channels in the guard cell plasmalemma (MacRobbie 1998). It causes inhibition of the activity of proton pumps in plasmalemma, depolarization of plasma membranes and opening of channels for potassium and anions (Ishkawa et al. 1983). After depolarization of the membranes, potassium is no longer retained by the negative bioelectric potential in the cells and passes through diffusion into the adjoining cells, followed by water exosmosis, loss of guard cell turgidity and hydro active closure of the stomata.

The presence of abscisic acid in the root cells is received by soluble sensors, made up of three proteins, which have received the name: PIR/PYL/RCAR. Activation of these receptors can activate the Ca^{2+}-dependent protein kinase chain and transcription

factors and determines the expression of genes involved in the response to water stress only in the presence of endogenous abscisic acid, while other genes respond both to the action of water stress and in the absence of this hormone (Shinozaki and Yamaguchi-Shinozaki 1999). Shinozaki and Yamaguchi-Shinozachi (1999) note that thermohydric stress causes the induction of genes encoding enzymes involved in the synthesis of proteins with a protective role hormones (abscisic acid), (thermal stress proteins HSP, LEA-proteins, osmotin), osmoprotective substances (soluble carbohydrates, proline, glycine, polyols, etc.), aquaporins involved in the transport of water through plasma membranes, enzymes involved in cell detoxification (catalase, superoxide dismutase, glutathione-S-transferase) and antioxidants.

1.1.3.6 Heat Shock Proteins

Moderate heat shock allows plants to acclimatize and survive in conditions of more severe heat stress through the synthesis of heat shock proteins. Vierling (1991) estimates that 1–2 h after the action of thermal stress on plants, the expression of heat shock protein (*HSP)* genes takes place, which determines the rapid synthesis of a new messenger RNA encoding new proteins (HSPs), thermal shock proteins. The high soil temperature (35–40 °C) stimulated the synthesis of 14 heat shock proteinsin resistant varieties of beans and only six proteins in the sensitive ones (Michiels 1994). The presence of these proteins has been identified in mitochondria, chloroplasts, and the endoplasmic reticulum. They have a molecular weight between 10 and 114 kDa and were classified according to molecular weight in five families, depending on molecular weight.

The role of HSP is diverse. Thus, heat shock proteins in mitochondria and chloroplasts protect the electron transport chain, some prevent the aggregation of proteins in cells, others promote their replication, help stabilize partially unfolded proteins, participate in achieving specific conformation of proteins. HSP bind to proteins that due to stress do not have the natural conformation, modify this conformation in the presence of ATP, release the protein, which in the presence of another HSP returns to normal structure (Mahmood et al. 2010). Thermal shock proteins have the role of molecular chaperones that prevent the aggregation of proteins, recognize, and bind denatured proteins in the inactive stage and promote their replication.

Neumann et al. (1995) specified that HSP form granules in the cytoplasm that stabilize the proteins and prevent their irreversible aggregation. Harndahl (1999) found that plants exposed to high temperatures synthesize thermal shock proteins with a molecular mass of 21 kDa, which prevents the aggregation of proteins, and after Lee et al. (1997) they keep them in non-negative form, the state in which they can be folded again. These stabilized proteins can return to the native form, through a folding mechanism, in which the HSP-70 protein is involved (Lee and Vierling 2000). During severe stress, insoluble complexes form. The role of HSP-100 proteins is to resolubilize these aggregates and transfer proteins released from insoluble complexes to the HSP-70/HSP-40 folding mechanism (Schirmer et al. 1996). Gurley (2000) notes that Hsp-100 is not used by all organisms to solubilize

protein aggregates and in some species, the role of HSP-100 proteins is taken over by lower molecular weight HSP proteins.

HSP have been identified in many horticultural plants, which have been exposed to moderate heat stress. Sanchez et al. (1992) consider that severe thermal stress, which is usually lethal to plants, can be tolerated for short periods of time if they were initially exposed to pre-adaptation. This consists of prior exposure to conditions of moderate stress, which determines the synthesis of the HSP-101 protein, and optimizes thermotolerance.

Souza et al. (2011), concluded that the action of an increase in temperature above the critical value for a specific period can cause irreversible damage. In this way it was reconfirmed the fact the tolerance limit of the plant under temperature stress may vary according to different factors as species, genotype, the phenological phases of the same species and genotype.

1.1.3.7 Late Embryogenesis Abundant (LEA) Proteins

Drought-induced osmotic stress causes the synthesis of LEA proteins that are synthesized and accumulated in seed embryos, during their maturation period (seed dehydration), as well as in various plant tissues exposed to water stress. These proteins have a low molecular weight (10–30 kDa). In plants exposed to water stress, saline stress, stress caused by low temperatures and in response to the action of abscisic acid they accumulate in greater quantities in the nucleus (Goday et al. 1994), in the endoplasmic reticulum (Lee et al. 2000), in plastids, in the cytoplasm (Rorat 2006), but also in plasma membranes. The accumulation of these substances contributes to the achievement of tolerance to dehydration. They are considered as intrinsic, hydrophilic, unstructured proteins and have no secondary or tertiary structure. They have a high degree of hydrophilicity and can bind water, reducing its loss under stress.

Dehydrins are *LEA* proteins, synthesized by the *Dhn* gene family and have the role of retaining water in cells, protect the structure of membranes and prevent clotting of cellular proteins under conditions of water stress and maintain the structural integrity of cells (Campbell and Close 1997). The presence of LEA18 proteins, from group 4, with a molecular weight between 8.4 and 18.8 kDa, was identified in bean plants. These proteins can bind to membranes, maintaining their structural integrity, and can bind ions, protecting the cytoplasm from the negative effect of their excess. The role of *LEA* proteins has not yet been well defined. It is estimated that the disordered structure of these proteins gives them a high reaction rate, form reversible bonds and may play a role in transmitting information at the cellular level (Kovács et al. 2008). These proteins have the role of protecting cellular structures, or restoring them, after the action of water stress. According to Ingram and Bartles (1996), severe water loss from cells causes changes in the structure of cytoplasmic proteins, and *LEA* proteins can maintain the structure under conditions of water stress.

1.1.3.8 Synthesis of Osmotically Active Substances

The absorption of water by plants from the soil solution is achieved through a process of endosmosis. In drought conditions, the concentration of soil solution increases, which prevents the absorption of water by plants and causes a process of exosmosis. Acclimatization of plants to drought conditions can be achieved by increasing the osmotic potential of root cells, by synthesizing and accumulating osmotically active substances, such as: carbohydrates (glucose, fructose, sucrose), amino acids (proline, serine, asparagine), organic acids (oxalate, malate) and small amounts of mineral ions. The accumulation of these substances causes the concentration of cellular juice, the decrease of osmotic potential, which ensures the plants the ability to absorb small amounts of water from dry soils. It follows that the osmotically active substances are represented by organic compounds and to a lesser extent by inorganic compounds. Of these, high concentrations of ions can cause adverse reactions in plants, which affect metabolic processes. For this reason, organic compounds are the most important osmoregulatory compounds in the plant world. Osmoregulatory substances accumulate in the cytoplasm or vacuole and facilitate osmotic adjustment and maintenance of cell turgor.

1.1.3.9 Aquaporins Synthesis

Water transport in plant root cells takes place among the phospholipid molecules that make up plasma membranes, but can take place at a higher rate through specialized water channels: aquaporins. Aquaporins are found in both plasmalemma (PIP) and tonoplast (TIP) and are protein tetramers that delimit a pore. Their synthesis is genetically coded and under conditions of water stress, the number of aquaporins increases, favoring the absorption and transport of water through the plant (Fray et al. 1994). Aquaporins also participate in the rapid hydration of cells and in the restoration of cell turgor, in the cessation of water stress. Increasing the number of aquaporins in the plant root cell plasmalemma, under conditions of water stress, is considered as an adaptation to faster water absorption.

1.1.4 Perspectives

According to different studies heat stress was estimated to be the most constraint abiotic stress, responsible to severe limitation of yields at global level due to the climatic changes.

CGIAR reported in 2015 that in Africa and Latin America, the production of beans is highly vulnerable to climate change impacts, which include higher temperatures and more frequent drought. Within the last 15 years, CGIAR researchers have registered key advance—particularly the development of drought-tolerant and

disease-resistant varieties—that will help make production more resilient in the face of future threats.

Current approaches aimed to develop tolerant and resistant genotypes involve obtaining transgenic plants featured by different tolerance traits. The benefits are related to shorter time as compared to classical breeding programs. For this goal, environmentally-controlled experiments need to be validated in long-term field experiments and this approach decrease severely the real advantage between the genetic approaches over the classical breeding. Moreover, legal limitations exist related to cultivation of transgenic plants in field, it remains arguable whether transgenic plants produced under controlled conditions to enhance tolerance really perform in field experiments in which other confounding variables may occur (Kapoor et al. 2020).

Population growth results in an increase in the absolute number of the population and an increase in the standard of living. These two determinants are associated with extraction and consumption of natural resources. The emission of greenhouse gases (GHGs) is a function of total population because every mouth must be fed. The growing population is putting stress on agricultural production systems that aim to secure food production (Vetter et al. 2017a, 2017b). On the contrary, food production contributes a substantial amount of GHGs, including carbon dioxide (CO_2), methane (CH_4) and nitrous oxide to the atmosphere (Steinfeld et al. 2006; Pitesky et al. 2009; Cohen 2010; Wolf et al. 2010a, 2010b; Vetter et al. 2017a, 2017b). Agriculture has a noteworthy contribution to ensure national food security, especially for developing countries. Methane generated from agricultural practices is the second major source of GHGs emission in the world (United States Environmental Protection Agency [USEPA] 2018). Furthermore, industrialization and development interventions contribute enormous GHGs emissions (He 2014). GHGs are the most important driver of observed climate change on Earth since the mid-twentieth century (USEPA 2018). In sober fact, the more population on Earth indicates more consumption and more emissions, which intensifies climate change.

Climate change is the single most pressing environmental issue for the Earth's biotic environment with adverse implications for food security, freshwater supply and human health (United Nations Framework Convention on Climate Change [UNFCCC] 2007). Climate change is also the biggest challenge for tropical and subtropical countries of the world, especially for coastal areas and islands. The impact would be particularly severe in the tropical areas, which mainly consist of developing countries (Sathaye et al. 2006).

Population includes the number of people; their demographic characteristics like age, sex, health, education and familial status; their demographic processes like birth, death, migration, the formation of unions and families and their dissolution; and the spatial distribution of people by geographic regions and size of settlements, from rural to urban (Cohen 2010). Therefore, population growth has diversified effects on development. On the contrary, the relationship between climate change and development is reciprocal. Social and economic development may be influenced by climate change, while society's precedence on sustainable development influences the level of emissions of GHGs that are causing climate change (IPCC 2007).

1.2 Description on Different Biotic Stresses

Dry beans are susceptible to biotic and abiotic stresses and depending on the severity of the stress and the plant's ability to tolerate them, yield can be severely affected. Biotic constraints such as fungal, bacterial, viral diseases and other diseases as well as insect pests, can cause serious yield losses especially when the climate is conducive to their development. Depending on the occurrence and severity of individual and collective diseases occurring in the same field, yield losses can range from 20 to 100% (Singh and Schwartz 2010). Variables such as production systems, management practices, cultivar choice and crop stage will all play a role in not only yield loss, but also quality of harvested seed, germinability, and its market value.

1.2.1 Antrachnose

It is caused by *Colletotrichum lindemuthianum* (Sacc. et Magn.) Briosi and Cavara. and is one of the most important diseases that affect common bean cultivars, especially in regions with moderate to cold temperatures (17–24 °C and relatively high humidity of more than 92% (Pastor-Corrales and Tu 1989; Thomazella et al. 2002). This disease can cause losses of up to 100% under favorable environmental conditions (Singh and Schwartz 2010). All aboveground parts of the plant can be affected. The first sign of the disease can be noticed as a brick-red discoloration along the veins on the lower surfaces of the leaves. Discoloration can be seen at a later stage on the upper surface of the leaves and petioles can also be affected. Symptoms on the pods begin as small brown spots that later enlarge to brown sunken lesions with a reddish-brown border. Symptomless seed infections will infect the hypocotyl. Survival of *C. lindemuthianum* in the debris of infected dry bean crops has been reported by Dillard and Cobb (1993) and Ntahimpera et al. (1997). Therefore, crop rotations of 2–3 years with non-host species is generally recommended as an important component in the integrated control of anthracnose (Dillard and Cobb 1993; Schwartz et al. 2005). Seed-borne transmission of anthracnose fungus is an important factor in the spread of the pathogen to new bean producing regions of the world, as well as between fields in a growing region and can result in the introduction of new races into a region (Tu 1992; Conner et al. 2009).

Genetic resistance can minimize production costs and reduce damage to the environment (Falleiros et al. 2018). However, the large virulence diversity of *C. lindemuthianum* with hundreds of races (Pastor-Corrales et al. 1995) limits disease control and development of new cultivars with durable resistance (Pinto et al. 2012; Gilio et al. 2020). The races of the anthracnose pathogen comprised two separate groups based on their virulence; one group called Andean, causes disease only on cultivars from the Andean gene pool of common bean. The second group, designated Mesoamerican, causes disease on both Andean and Middle American cultivars; however, it is more virulent on cultivars of The Middle American gene pool (Pastor-Corrales et al.

1995; Pastor-Corrales 1996). Anthracnose resistance in common bean is conferred by multiple single, independent and mapped genes. Most of these genes have been assigned the *Co*-symbols, as follows: *Co-1* (with four alleles), *Co-2*, *Co-3* (with four alleles), *Co-4* (with two alleles), *Co-5* (with one allele), *Co-6*, *Co-11*, *Co-12*, *Co-13*, *Co-14*, *Co-15*, *Co-16*, and *Co-17*. With the exception of the recessive *Co-8* gene, all other genes are dominant genes (Kelly and Vallejo 2004; Gonçalves-Vidigal et al. 2011; de Lima et al. 2017; Valentini et al. 2017, Gilio et al. 2020). The nine resistance genes Co-2 to *Co-6*, *co-8*, Co-11, *Co-16* and *Co-17* are Middle American in origin and *Co-1, Co-12* to *Co-15*, and *Co-AC* (Gilio et al. 2020; Valentini et al. 2020) are from the Andean gene pool. An order of dominance exists among the four alleles at the *Co-1* locus.

1.2.2 Angular Leaf Spot (ALS)

It is caused by the fungus *Pseudocercospora griseola* (Sacc.) Crous et al. (2006). Several articles reviewing the most important aspects of the ALS disease and genetic studies to find resistance loci in common bean have been published (Correa-Victoria et al. 1989; Liebenberg and Pretorius 1999; Nay et al. 2019). The ALS disease has been reported occurring in all continents but Antarctica (Zaumeyer and Thomas 1957; Liebenberg and Pretorius 1997; Correa-Victoria et al. 1999; Stenglein and Balatti 2006; Aggarwal et al. 2003). However, ALS is a particularly recurrent, severe and widely distributed disease in tropical and subtropical areas, especially in South and Central America, Mexico, the Caribbean, and in Eastern and Southern Africa (Correa-Victoria et al. 1989; Liebenberg and Pretorius 1997; Aggarwal et al. 2004; Nay et al. 2019). ALS also occurs on dry beans produced in temperate regions (Correa and Saettler 1987; Melzer and Boland 2001; Landeras et al. 2017).

While ALS occurs predominantly on dry beans, it has also been reported occurring on French (snap) beans in Africa (Kimno et al. 2016). The ALS disease affects aerial parts of the common bean plant, particularly foliage and pods, during the growing season. Temperatures between 17 and 24 °C, with an optimum of 24 °C, and high humidity favor the development of the ALS disease. The characteristic symptoms on leaves initially are small brown and gray lesions between the leaf veins that become necrotic and that later assume an angular shape, which is the typical symptom of the ALS disease on the foliage. Stems often are covered with necrotic spots. The symptoms on the pods appear as dark reddish brown and often round, roughly circular lesions, frequently covered with sporulation of the ALS pathogen. Sporulation is also common on the lower side of the leaves. In general, ALS tends to be most destructive during and after flowering, causing premature defoliation, reduced seed size and quality that can result in severe yield losses reaching 80% (Schwartz et al. 1981; Rava Seijas et al. 1985; de Jesus Junior et al. 2010). Volunteer plants, off-season crops and ALS infected plant debris have been reported as the principal sources of inoculum (Correa-Victoria et al. 1989). Infested seed can also cause infections but is generally not regarded as an important source of inoculum (Liebenberg and

Pretorius 1997). Planting pathogen-free seeds treated with effective fungicides, crop rotations, and use of foliar fungicides have been reported as options to control the ALS disease; however, fungicides are often expensive or not readily available to smallholder farmers, the predominant producers of common bean in the tropics. Hence, planting cultivars with resistance to *P. griseola* present a cost-effective, easy to use, and environmentally friendly strategy to manage the ALS disease (Pastor-Corrales et al. 1998; Aggarwal et al. 2004; Gonçalves-Vidigal et al. 2011, 2013). Nevertheless, resistant varieties may become susceptible due to the appearance of new virulent strains, known as races, of *P. griseola.* Due to the appearance of new races, varieties that previously were resistant in a given year or location can suddenly become susceptible.

The ALS pathogen is known for its extensive virulence diversity that comprises hundreds of different virulent races (Pastor-Corrales et al. 1998; Busogoro et al. 1999; Mahuku et al. 2002; Sartorato 2004; Aggarwal et al. 2004; Stenglein and Balatti 2006; Nay et al. 2018). These races are identified by inoculating each isolate on an internationally accepted set of 12 differential cultivars, six Andean and six Mesoamerican cultivars, developed by Pastor-Corrales (1996). The large number of races of *P. griseola* separate into two distinct virulence groups; Andean races infecting only Andean differential cultivars and Mesoamerican races, infecting Mesoamerican and Andean differential cultivars (Guzman et al. 1995; Pastor-Corrales 1996; Mahuku et al. 2002; Aggarwal et al. 2004). Resistance to the ALS pathogen is conferred by several single dominant resistance loci and quantitative resistance loci (QTLs) as reviewed by Nay et al. (2019). Currently five ALS resistance genes have been given official names (Souza et al. 2016). These include three dominant and independent *Phg* loci named *Phg-1* [present in Andean (A) common bean AND 277], *Phg-2* [present in Mesoamerican (MA) common bean Mexico 54] and its allele Phg-2^2 (present in MA common bean BAT 332), *Phg-3* (present in MA common bean Ouro Negro) and two major quatitative trait loci (QTLs) named *Phg-4* (present in A common bean G5686) and *Phg-5* (present in A common beans CAL 143 and G5860 (Gonçalves-Vidigal et al. 2011, 2013; Oblessuc et al. 2012, 2013; Keller et al. 2015; Nay et al. 2019). Several molecular markers linked to these resistance loci are available and can be used to efficiently incorporate the resistance loci in new bean varieties (Nay et al. 2019).

1.2.3 Rust

The common bean rust disease is caused by the basidiomycete fungus *Uromyces appendiculatus* (Pers.: Pers.) Unger. This disease has worldwide distribution and occurs in most dry and snap bean growing areas of the world and particularly in locations with cool temperature (17–22 °C) and high humid conditions (>95%) maintained for 8–10 h and long dew periods. Rust is rare in arid climates except under irrigation. Bean rust has been reported occurring throughout Latin America where it is an important disease in Brazil, Central America, Mexico, and the Caribbean. It also

has been reported in multiple countries of Eastern and Southern Africa. In addition to infecting dry beans, the rust pathogen also infect snap bean where it is often a recurrent and severe disease of snap beans grown in East Africa, Latin America and Asia (Zaumeyer and Thomas 1957; Stavely and Pastor-Corrales 1989). Yield losses depend on the climatic conditions favoring rust development, and the earliness and severity of the infection. Infections occurring during the pre-flowering and flowessring stages usually result in high to extremely high yield losses approaching 100%. High losses have been reported in many countries of the Americas, Africa and other geographic areas (Stavely and Pastor-Corrales 1989).

The bean rust pathogen is an obligate parasite of common bean and it cannot live independently of its host. This fungus cannot be cultured on artificial media; thus, it depends on wild and cultivated common beans for its survival. This pathogen has a complex life cycle that includes five different spore stages and three nuclear conditions (Groth and Mogen, 1978; McMillan et al. 2003), which are suggestive of its capacity for genetic recombination. The entire life cycle is completed on common bean. The rusty cinnamon brown pustules present on the foliage of common beans during the planting season, gives the disease its "rust" name. The pustule or uredinia which occur on leaves, stems and pods, contain thousands of spiny cinnamon brown spores named urediniospores. Repeated generations of urediniospores happen during the growing season. Toward the end of the growing season and under appropriate conditions, the next spore stage is named telia that develops within the aged uredia and produces dark brown, nearly black, ovoid teliospores. The other three spore stages occur later but are not easily seen. Many publications have revealed the extensive virulence diversity of this pathogen. Hundreds of different virulent races of *U. appendiculatus* have been reported around the world (Stavely 1984; Stavely and Pastor-Corrales 1989; Stavely et al. 1989; Araya et al. 2004; Acevedo et al. 2012; Arunga et al. 2012). Different races produce dissimilar virulent phenotypes when they are inoculated on a set of differential cultivars. A new set of 12 differential cultivars, created by Pastor-Corrales, containing six Andean and six Middle American cultivars was approved for international use during the 2002 International Bean Rust Workshop that took place in South Africa (Steadman et al. 2002). This new set replaced the previous set containing 19 differential cultivars that was adopted during the 1983 Bean Rust Workshop held at Mayaguez, Puerto Rico (Stavely et al. 1983). In addition to adopting a new set of 12 differential cultivars, it was also agreed to name the new races of *U. appendiculatus* using a "Binary System" in which each of the six Andean and six Middle American cultivars were assigned a numeric value. The name of each race included two digits separated by a hyphen.

These two numbers specify which rust resistance genes present on the differential cultivars were susceptible. Using this new set of differential cultivars and molecular markers, the races of the bean rust pathogen have been segregated into two different groups, one Andean and another Mesoamerican that correspond to the Andean and Middle American gene pools of the common bean, respectively (Pastor-Corrales and Aime 2004). Genetic resistance is the most cost-effective strategy to manage the bean rust pathogen. Rust resistance in common bean is conferred by single and dominant genes identified by the Ur- symbol (Kelly et al. 1996). Currently, 10 rust

resistance genes have been named, mapped and tagged mostly with random amplified polymorphic DNA (RAPD) and sequence characterized amplified region (SCAR) molecular markers (Miklas et al. 2002; Hurtado-Gonzales et al. 2017). Six genes (*Ur-3, Ur-5*, *Ur-7, Ur-11, Ur-13*, and *Ur-14*) are present in common beans that belong in the Middle American gene pool, while the other four genes (*Ur-4, Ur-6, Ur-9*, and *Ur-12*) are in common beans belonging in the Andean gene pool. The Andean rust resistance genes are preponderantly susceptible to Andean races of *U. appendiculatus*; however, these genes often confer resistance to highly virulent Mesoamerican races. Conversely, the Middle American rust resistance genes are usually broader in their resistance spectrum than the Andean resistance genes and are very effective against most Andean races of *U. appendiculatus.* All rust resistance genes differ in their spectrum of resistance to the known races of the rust pathogen. None of these genes are either susceptible or resistant to all known races. The *Ur-11* gene present in the PI 181,996 accession has the broadest spectrum of resistance of all named rust resistance genes (Hurtado-Gonzales et al. 2017). Similarly, the *Ur-14* gene present in the Ouro Negro landrace is also broadly resistant (Souza et al. 2011.) Combining rust resistance genes from the Andean and Middle American gene pools results in broad spectrum resistance to all known races of *U. appendiculatus.*

The pinto bean germplasm line BelDakMi-RMR 18 and six great northern bean germplasm lines (BelMiNeb-RMR-8 to BelMiNeb-RMR-13), developed at the ARS-USDA Beltsville Agricultural Research Center, Beltsville, Maryland, USA, combine the Andean *Ur-4* and *Ur-6* and Middle American *Ur-3* and *Ur-11* rust resistance genes. All these seven lines have been evaluated as resistant under greenhouse conditions to more than 70 Andean and Mesoamerican races of the rust pathogen (Pastor-Corrales et al. 2007). These lines have also been evaluated as resistant to rust in small plots planted under field conditions in various dry bean producing states in the United States and in other locations including Puerto Rico, Honduras, Brazil South Africa, and other sites. These results support the proposition that combining rust resistance genes of Andean and Middle American origin can result in common bean cultivars with broad resistance to the highly virulence variable rust pathogen of common bean.

1.2.4 Rhizoctonia Solani *Kuhn. Teleomorph:* Thanatephorus cucumeris *(A. B. Frank) Donk*

It is a heterogenous multinucleate species complex that includes 15 anastomosis groups (Carling et al. 2002; Godoy-Lutz et al. 2008; Bolton et al. 2010) based on hyphal fusion, cultural morphology, pathogenicity, or virulence and DNA homology (Godoy-Lutz et al. 2003; Harikrishnan and Yang 2004). The diversity of this soil-borne pathogen is a major reason for the difficulty in managing *R. solani* root rot. *R. solani* can occur during any stage of the common bean growth stage (Valentín Torres et al. 2016). It can cause severe plant diseases which can differ in symptomology like collar rot, root rot, damping off and wire stem (Ogoshi 1996) as well as complete

defoliation, leading to complete crop failure (Singh 2001). Because of its facultative parasitic ability, it can survive as a saprotroph (Zhao et al. 2005) in the form of sclerotia on infected plant debris. *R. solani* then act as an inoculum for susceptible plants such as sugar beet (*Beta vulgaris* subsp. vulgaris) (Plyler-Harveson et al. 2011), dry beans (*Phaseolus vulgaris*) (Das et al. 2020), potato (*Solanum tuberosum*) (Wendels et al. 2009), and soybean (*Glycine max*) (Liu and Klein 2012). *R. solani* can also spread by airborne basidiospores (produced by the teleomporph *T. cucumeris*) as well as mycelial bridges between plants and infected seed (Godoy-Lutz et al. 2003). Hagedorn (1994) and Singh and Schwartz (2010) reported that *R. solani* severely impacts seed yield of common bean, resulting in upwards to 100% seed yield loss.

Although genetic resistance is considered the most cost effective and sustainable management of root rots in common bean (Abawi and Pastor-Corrales 1990; Park and Rupert 2000; Abawi et al. 2006), sources with resistance is limited. Oladzad et al. (2019) reported evidence for major as well as minor genes involved in resistance to *R. solani* in common bean. According to Harman et al. (2004) and Siameto et al. (2011), *T. harzianum* inhibit fungal growth through competition for space and nutrients, mycoparasitism and production of antibiotic compounds. Matloob and Juber (Matloob and Juber 2013) reported that *A. chroococcum*, *G. intraradices* and *T. harzianum* decreased *R. solani* root rot disease incidence (field trials) and increased plant resistance against infection with *R. solani* and improve plant growth and yield.

1.2.5 Pythium

It is a complex genus containing over 200 described species with a broad host range and occupying a variety of terrestrial and aquatic ecological habitats (Dick 2001). *Pythium* spp. that cause root rot of common bean can be found worldwide (Paul 2004). An increase in root rot producing *Pythium* spp. have been reported over the last 20 years in countries such as Eastern and Central Africa, Burundi, the Democratic Republic of Congo, Kenya and Uganda (Otsyula et al. 2003). For example, in Western Kenya and in Rwanda, many farmers stopped growing beans between 1991 and 1993 due to a severe outbreak of root rots, which caused serious food shortages and price increases beyond the reach of many resource-poor households (Nekesa et al. 1998).

Depending on the *Pythium* spp. involved, symptoms can include general root rot symptoms, any combination of various traits such as poor seedling establishment, damping-off, uneven growth, leaf chlorosis, premature defoliation, death of severely infected plants and lower yield (Abawi et al. 2006; Schwartz et al. 2007). *Pythium* spp. can reproduce both asexually and sexually. Asexual reproduction takes place through the zoosporangia and zoospores (Nzungize et al. 2012). Structures such as oospores, zoospores and sporangia enable this species to survive in soil for long periods (Onokpise et al. 1999). There are many specific pesticides such as benomyl, captafol, captan, carboxin, metalaxyl, propamocarb hydrochloride and etridiazole, which have already proven to be efficient in controlling Pythium root rot diseases

on beans. However, some pesticides, such as benomyl, are only active on growing mycelium, but not during the resting stage of the mycelium (Nzungize 2012).

The coating of bean seeds usually results in effective protection of seeds and young seedlings for about 2–3 weeks after sowing (Abawi et al. 2006; Schwartz et al. 2007). Beneficial microorganisms of interest for biological control of plant pathogenic *Pythium* spp. have been identified among fungi and bacteria. Isolates of *Trichoderma* spp. and *Gliocladium* spp. are antagonists of Pythium induced soil-borne diseases and several strains are already commercially available for the biological control of Pythium root rots (Howell et al. 1993; Fravel 2005). Although the use of resistant common bean cultivars can be the most efficient management strategy against root rot diseases, these cultivars should have resistance to all the major root rot pathogens that prevail in a given bean growing region (Abawi et al. 2006). Cultural practices such as deep plowing and the use of raised ridges to grow beans has been found to reduce root rots favored by high moisture (Rhizoctonia, Fusarium and Pythium root rots) (CIAT 1992).

1.2.6 Fusarium Root Rot

It is caused by *Fusarium solani* (Mart.) Sacc. f. sp. *phaseoli* W.C. Snyder and H.N. Hansen, has been considered as one of the major yield-limiting diseases of dry bean worldwide (Kraft et al. 1981; Bilgi et al. 2008; Mwang'ombe et al. 2008). *F. solani* is commonly found as part of a complex with *Rhizoctonia solani* and *Pythium* spp. Fusarium root rot can cause severe yield losses, especially when adverse environmental conditions (such as soil moisture and soil compaction) persist after planting and at flowering stage (Román-Avilés et al. 2003). Unlike other root-rotting diseases, *F. solani* does not cause seed rot, or damping off of seedlings. Symptoms of Fusarium root rot on common bean are narrow, dark brown to rust colored lesions on the stems where lengthwise cracks can develop. Lesions extend down the main taproot (Román-Avilés et al. 2003) and can cause shriveling decay and death of the taproot. Lateral roots or adventitious roots commonly develop above the shriveled taproot and under ideal growth conditions, they can limit above ground symptoms. When lesions on the lower hypocotyl coalesce as the disease progress, it can result in complete rot of the root system (Abawi 1989). When left unmitigated, Fusarium root rot can cause up to 84% yield loss (Schneider et al. 2001).

Managing Fusarium root rot can be difficult due to the durability and extended viability of chlamydospores in soil and plant debris (Katan 2017). Current management strategies include the use of seed treatment chemicals, avoiding infested fields, croprotation, and planting certified seeds. However, the most sustainable and durable approaches for controlling the disease is genetic resistance (Rubiales et al. 2015). While foliar disease resistance is a target for crop improvement, less emphasis has been given to breeding for root rot resistance in common bean and there were fewer sources of root rot resistance available.

Because of this paucity and a shift in research focus, authors from multiple studies have characterized and identified sources of resistance within common bean germplasm collections (Román-Avilés and Kelly 2005; Bilgi et al. 2008; Nicoli et al. 2012; Hagerty et al. 2015; Nakedde et al. 2016; Vasquez-Guzman 2016).

The high variability in cultural characteristics exhibited by *F. solani* f. sp. *phaseoli* isolates (Nelson et al. 1983; Nirenberg 1989) poses a challenge to efforts aimed at breeding for resistance to bean root rot disease. Moreover, host specificity (Li et al. 2000) as well as a ribosomal DNA nucleotide sequence (Suga et al. 2000) has shown that *phaseoli* is a very diverse form, almost indiscernible from other related forms such as *glycines*. In general, cultivars developed from the large-seeded Andean gene pool such as red kidney bean tend to be more susceptible to Fusarium root rot than those developed from the small-seeded Mesoamerican gene pool, such as black bean (Beebe et al. 1981).

1.2.7 White Mould

It is caused by *Sclerotinia sclerotiorum* (Lib.) de Bary and is a major disease concern for bean growers in cool subtropical and temperate climates where moist conditions prevail due to irrigation or rainfall (Miklas et al. 2006). It is a highly destructive disease, affecting both dry bean yield and quality (Pynenburg et al. 2011). White mold symptoms can be observed on all aerial plant parts (Schwartz and Singh 2013). Infected flowers may develop a white, cottony appearance as mycelium grows on the surface. Lesions on pods, leaves, branches, and stems are initially small, circular, dark green, and water soaked but rapidly increase in size, may become slimy, and may eventually encompass and kill the entire organ. Under moist conditions, these lesions may also develop a white, cottony growth of external mycelium. Affected tissues dry out and bleach to a pale brown or white coloration that contrasts with the normal light tan color of senescent tissue (Schwartz and Singh 2013). The epidermis easily sloughs off when the stem or pod is rubbed. Entire branches or plants may be killed (Steadman and Boland 2005).Colonies of white mycelium (immature sclerotia) develop into hard, black sclerotia in and on infected tissue. Sclerotia (approximately 5–10 mm long) allow the fungus to survive in a dormant state for periods of months to years (Koike et al. 2007), providing primary inoculum for successive susceptible crops.

In bean, the dominant mechanism of sclerotial germination is carpogenic, during which stipes push to the soil surface and form small, tan, cup-shaped apothecia that produce copious numbers of wind-borne ascospores (Willetts and Wong 1980). Primary infections in bean, are most commonly by ascospores infecting senescent flower tissue, which is subsequently colonized by the fungus. The senescent tissue provides the fungus with an energy source for later infection of healthy tissues (Abawi and Grogan 1979). Secondary spread within the canopy may occur when infected petals fall and make contact with other plant parts, including pods, leaves or stems (Abawi and Grogan 1979). White mould is difficult to control due to a wide host

range and the ability of the fungus to survive for long periods as sclerotia. There is a lack of commercially suitable bean cultivars with resistance (Jones et al. 2011). The combination of genetic resistance with avoidance mechanisms, including upright and open plant structure, less dense canopies and branching patterns, elevated pod set, and reduced lodging (Schwartz et al. 1987), is the current breeding strategy for reducing white mold damage in dry bean (Kolkman and Kelly 2002).

1.2.8 Bacterial Diseases

They include common bacterial blight caused by *Xanthomonas axonopodis* pv. *phaseoli* (Smith) Vauterin et al. and *Xanthomonas fuscans* subsp. *fuscans*, (recently reclassified by Constantin etal. (2016) as *X. phaseoli* pv. *phaseoli* and *X. citri* pv. *fuscans*, respectively), halo blight (*Pseudomonas savastanoi* pv. *phaseolicola*) (Burkholder) Gardan et al., bacterial brown spot (*Pseudomonas syringae* pv. *syringae*), van Hall, and bacterial wilt *Curtobacterium flaccumfaciens* pv. *flaccumfaciens* (Hedges, Collins and Jones). Pathogenic variation exist within the halo blight pathogen, with nine races reported worldwide (Taylor et al. 1996). Despite several reports on pathogenic variation within the common blight pathogen, no evidence for the existence of races have been reported using common bean differential lines (Mutlu et al. 2008). Bean bacterial diseases are seed-borne and affect foliage, stems, pods and seeds of beans (Yoshii 1980) with losses of up to 45% reported (Singh and Schwartz 2010). Effective and economical control of bacterial diseases can only be achieved using an integrated approach, including cultural practices, chemical sprays and genetic resistance. Planting of pathogen-free seed is the most important primary control method (Gilbertson et al. 1990), however, it does not guarantee disease control (Allen et al. 1998). Additional cultural practices such as removing, destroying or deep ploughing of debris, effective weed control, crop rotation and minimized movement in fields, especially when foliage is wet, may be effective (Allen et al. 1998; Schwartz and Otto 2000). Copper-based bactericides protect foliage against bacterial diseases and secondary pathogen spread. Efficacy of chemical control, however, is limited (Allen et al. 1998) and resultant yield increases are minimal (Saettler 1989). The most important factor of an integrated approach is use of resistant cultivars. Singh and Schwartz (2010) recently reviewed the status of breeding for resistance to bacterial diseases and although significant progress has been made in identifying resistance genes, common bean cultivars with adequate levels of resistance are still lacking.

1.2.9 Diseases Caused by Viruses

Bean Common Mosaic Virus (BCMV) and Bean Common Mosaic Necrosis Virus (BCMNV)

They belong to the genus Potyvirus; Potyviridae are closely related. They induce similar symptoms in bean, and exist as a complex of strains with multiple isolates which differ in their virulence on common bean cultivars. BCMV and BCMNV can be disseminated by seed and vectors such as aphids and leaf beetles. Seed transmission of BCMV can range from 18 to 80% (Hall 1991; Klein et al. 1994; Bashir et al. 2000). Wild plants and weeds can act as virus reservoirs for transmission by vectors, as demonstrated by infection of wild legume species with BCMV (Flores-EsteÂvez et al. 2003; Melgarejo et al. 2007; Nordenstedt et al. 2017). Even with low seedborne transmissions, severe disease epidemics can be expected when combined with the efficient spread by vectors to susceptible cultivars (Johansen et al. 1994). BCMV and BCMNV are the most common and destructive viruses and the interaction between bean variety, virus strain and time of infection, will determine yield losses. Hall (1991) and Bashir et al. (2000) reported yield losses of up to 15% in plants of cv. Red Mexican U.I.34 that were either moderately or severely infected. Pod yields were reduced by 50 and 64% and seed yields were reduced by 53–68% respectively.

BCMV and BCMNV isolates are classified into seven pathotypes according to their reactions on 12 to 14 bean differentials with known combinations of resistance genes (Drifjhout 1978). Necrotic strains evolved more recently in the African continent (Spence and Walkey 1995) as recombination between strains of BCMV and BCMNV has been reported (Larsen et al. 2005). Five resistance genes govern interactions of BCMV and BCMNV isolates with common bean—one strain-nonspecific dominant I gene, and four strain-specific recessive genes: *bc-u*, *bc-1*, *bc-2*, and *bc-3* (Drifjhout 1978). If a BCMNV isolate is inoculated into an I-gene-carrying cultivar, a necrotic reaction occurs, regardless of the temperature, varying from limited vein necrosis on the inoculated leaf to a severe, whole-plant necrosis, called "black root syndrome". This reaction is called temperature-insensitive necrosis (TIN). When such necrotic reaction occurs, no virus replication is detected in leaf tissues surrounding necrotic tissue and no virus transmission through seed can be detected, resulting in a resistance reaction at the plant level (Feng et al. 2014).

1.2.10 The Bean Fly (Ophiomyia *Spp.)*

It is also known as the bean stem maggot and is considered as the most important insect pest of common bean. Though, it has been reported in Africa, Asia and Austria, it is widely distributed in Africa (Nkhata et al. 2019). The bean fly is a tiny insect of Agromyzidae family. The family consists of the following species: *Ophiomyia phaseoli* Tyron (*O. phaseoli*), *O. spencerella* Greathead (*O. spencerella*), *O. centrosematis* de Meij (*O. centrosematis*), *Melanagromyz sojae* Zehntner (*M. sojae*), *M.*

phaseolivora Spencer (*M. phaseolivora*) (Allen and Smithson 1986; Nkhata et al. 2019). The first three are considered as the most destructive, whereas the last two are either minor or occasional pest of common bean. Both the adult and larvae of the bean fly cause significant crop damage. However, the larvae causes the most significant damage (Kayitare 1993; Davies 1998). After oviposition under the surface of young bean leaves, larvae burrow under the thin layer of the leaf (epidermis), and tunnel along the veins down to the stem, and lodges where the stem touches the soil. Pupation takes place inside the bean stem, resulting in swelling and cracking of the stem at the point where the pupae are lodged, which destroys the transport system of the plant nutrients from the roots as well as products of photosynthesis from the leaves, leading to stunted growth, and yellowing of leaves at an early plant stage. Heavy infested crop stands are characterised by premature leaf drop and plant death (Davies 1998; Ojwang' et al. 2011). The occurrence and epidemic levels of the bean fly is dependent on suitable environmental conditions and availability of host plant species. High temperature, relative humidity and drought are reported to be favourable condition for bean fly. The pest causes up to 100% yield losses (Nkhata et al. 2021b).

Control strategies for bean fly includes, chemical pesticides, cultural practices, use of biological agents and host plant resistance. Chemical control method using seed dressing with sulphate based insecticides has been reported to be effective (Mutune et al. 2016). In addition, pesticides such as Gaucho 600 (active ingredient imidacloprid) and Pesthrin 6% EC (active ingredient pyrethrins) are used to control the bean fly at seedling or adult plant stages (Ambachew et al. 2015; Muthomi et al. 2018). Chemical insecticides are effective in controlling bean fly though they pose potential hazards to the ecosystem (Alavanja 2009). Chemical control expensive for majority of smallholder farmers (Laizer et al. 2019). Additionally, pesticide resistance can occur due to excessive use (Damalas and Eleftherohorinos 2011). Cultural practices such as early sowing, crop rotation, intercropping with maize, earthing up soil around the seedlings and fertilizer application are reported to control bean fly (Kapeya et al. 2005; Nkhata et al. 2021a). Early sowing allows the bean crop to avoid the insect pest in the field, while crop rotation and intercropping suppresses bean fly population in the field (Nkhata et al. 2021a). Earthing up promotes the development of new roots above the swelling caused by bean fly larva damage. The newly developed roots help to sustain the crop, while overcoming the impact of the damage whereas, fertilizer application ensures availability of nutrients for plant growth and maintenance of vigor (Nkhata et al. 2021a). Biological control involving the use of bean fly parasitoids such as *Opius phaseoli* Fisher and *O. importatus* suppress bean fly population but they are not very effective (Davies 1998). Incorporating host resistance is an effective, reliable and environment friendly method to control bean fly (Nkhata et al. 2021b).

Although host resistance is considered as the most effective control of bean fly. Resistance to bean fly in bean is still scarce despite decades of screening for resistance (Miklas et al. 2006; Nkhata et al. 2021b). Lack of a systematic screening procedures that exert uniform infestation of the genotypes has been the main attribute of scarcity of resistance (Hillocks et al. 2006). Bean fly resistance is quantitative and having

significant interaction with the growing environment (Mushi and Slumpa 1996; Wang and Gai 2001; Ojwang et al. 2011). Due to the high genotype-by-environment interaction, evaluation and selection of germplasm for bean fly resistance should be conducted under the target production environment (Nkhata et al. 2021b).

The resistance has been linked with morphological markers such as phenolic compounds, internode length, leaf hairiness, stem diameter and stem color in common bean and other related species (Rogers 1980; Abate 1990; Ambachew et al. 2015). Phenolic compounds serve as toxicants that inhibit the growth of bean fly (Chiang and Norris 1983). Narrow stem and short internode in common bean result into highly lignified stem, making it more difficult for the bean fly larvae to burrow into the stem (Abate 1990; Kayitare 1993; Ambachew et al. 2015). These morphological markers are useful under conventional breeding. Application of genomic tools have not be fully exploited in bean fly resistance such that there are few genomic studies on bean fly resistance compared to similar important traits in common bean (Miklas et al. 2006; Ojwang et al. 2019). The few genomic studies have mapped genes linked to bean fly on *B1, B2, B6, B8* and **B10** (Ojwang et al. 2019; Wilson Nkhata, unpublished data). The identified genomic regions offers prospects of genomic selection of bean fly resistance in common bean.

1.3 Genetic Resources of Resistance Genes

Nikolai Ivanovich Vavilov was a pioneer in recognizing the high potential value of plant genetic resources (PGR) for humankind. He highlighted the importance and potential value of collecting, conserving and exploiting the wide genetic diversity of crops and its wild relatives (CWRs) (Vavilov 1920, 1922). Harlan and de Wet (1971) formalized this particular issue by the introduction of the "gene pool concept", where crops and its related species can be divided into primary, secondary and tertiary gene pools according to how easy it is to use crop relatives in breeding (Maxted et al. 2006).

Diversity of germplasm stored in gene banks is a vital source for discovering useful genes that serve as a resource for common bean breeding programs. There are currently more than 1700 genebanks (FAO 2010), and more than 150,000 conserved *Phaseolus* accessions around the world (FAO Wiews 2019; Genesys 2020). The International Center for Tropical Agriculture (CIAT) in Columbia holds the largest *P. vulgaris* collection with 37,938 accessions, followed by the Western Regional Plant Introduction Station, United States Department of Agriculture (USDA-ARS) with 17,672 accessions, and the Brazilian gene banks Embrapa Arroz e Feijão, with 16,647 accessions, and Embrapa Recursos Genéticos e Biotecnologia, with 12,618 accessions. A great number of *Phaseouls* accessions are also held by theGerman gene bankLeibniz Institute of Plant Genetics and Crop Plant Research (IPK) with 9,004 accessions. Furthermore, the Russian collection of *Phaseouls*at the N. I. Vavilov Institute of Plant Genetic Resources (VIR) is one of the oldest in the world with 6,543 accessions.

Among the accessions, the following species are conserved: 135,582 *Phaseolus vulgaris*, 7,996 *Phaseolus lunatus*, 5,000 *Phaseolus coccineus*, 1,443 *Phaseolus acutifolius*, 629 *Phaseolus dumosus*, 224 *Phaseolus leptostachyus*, 127 *Phaseolus multiflorus*, 120 *Phaseolus* x *multigaris*, and some 2,000 accessions are unspecified species (*Phaseolus* sp.). The majority of the accessions are classified as traditional cultivar/landrace (82,742 accessions), followed by advanced/improved cultivar (20,720), wild (3,966), breeding/research material (1,667), breeders line (847), weedy (791), semi-natural/wild (150), natural (87), inbred line (76), and some 43,000 are not specified or specified as others (Genesys 2020). The top six countries of origin of the material are Mexico (10,650 accessions), Colombia (6,942 accessions), Brazil (6,737 accessions), Turkey (5,183 accessions), United States of America (4,986 accessions), and Peru (4,717 accessions).

At European level, the European Phaseolus Database (2020) was established in 1995 on the initiative of the European Cooperative Programme for Plant Genetic Resources (ECPGR) and holds in total 46,128 accessions from around 50 collection holders. Although the high number of total accessions, one-third of the global accessions (43,809 *Phaseolus* accessions) are not available for distribution, which highlight the challenges that many genebank have with backlogs and make accessions and information available. Morphological traits are often well described (for example, Fig. 1.1 shows variation in seed color) but to access resistance and tolerance traits, one often need to contact the collection holders or review published literature but collection holders try to make relevant information more accessible. For example, at CIAT (2020) there is a searchable facility for reactions to biotic and abiotic stresses with information on resistance to BCMV (Bean Common Mosaic Virus), and where 3,848 accessions (or around 10%) show up as resistant. So far, information on other reactions to biotic and abiotic stresses are not available online. This accounts from most genebanks although evaluations have been carried out. For example, the USDA genebank has data on resistance to Mexican bean beetle, BCMV, white mold (*Sclerotinia sclerotiorum*), Fusarium wilt (*Fusarium oxysporum* f. sp. *phaseoli*), rust *Uromyces phaseoli*, halo blight(*Pseudomonas syringe*),and bacterial wilt (*Curtobacterium flaccumfaciens*), but the data are not easily available.

1.3.1 Primary Gene Pool

The primary gene pool of common bean consists of *P. vulgaris* itself and its subspecies that are easy to interbreed, mainly *P. vulgaris* L. var. *aborigineus* (Burkart) Baudet.

Domestication of common bean took place at two places with the formation of the Mesoamerican and Andean types (Papa and Gepts 2003). Regarding abiotic stress, Beebe et al. (2012) reported that Durango lines originatedat higher altitude in semiarid zones of Mesoamerica had the highest drought tolerance. This type is therefore useful in breeding more drought tolerant cultivars (Terán and Singh 2002; Frahm et al. 2004). Here, the growth habit seems to influence the result and plants with indeterminate, prostrate habits tend perform relatively well under dry

Fig. 1.1 Illustration of the variation in seed coat color of Swedish accessions (Photo S.Ø. Solberg)

conditions (Beebe et al. 2013a). Furthermore, deep rooting is another advantage as well as small seed size, where accessions with a short seed-filling period are less exposed to stress than large-seeded accessions with a longer seed-filling period (Beebe et al. 2001). Regarding heat tolerance there is some of the same patterns. Small-seeded Mesoamerican types are often more tolerant than large-seeded Andean types (Beebe et al. 2013). A few exceptions exist: 'G122' and 'Indeterminate Jamaica Red', landraces from in India, and 'Sacramento' and 'Celrk', lines developed in California, show relatively high heat tolerance (Román-Aviles and Beaver 2003). In Lima bean, a similar relationship is found with Mesoamerican types having higher tolerance to abiotic stresses as heat and drought compared to large-seeded Andean types (Long et al. 2014).

1.3.2 Secondary Gene Pool

The secondary gene pool consists of taxa more remotely related to the crop but still possible to cross and give rise to some fertile progenies. According to Vincent et al. (2013), 36 crop wild relatives of *Phaseolus* are documented and have potential value as genetic resources for crop improvement. In the secondary gene pool, we find *P. albescens* McVaugh ex Ramirez-Delgadillo and A. Delgado, *P. coccineus* L., *P. costaricensis* Freytag & Debouck, *P. dumosus* Macfad, and *P. persistentus* Freytag and Debouck. Secondary gene pool has been used extensively as a source of disease resistance (reviewed in Porch et al. 2013) and to introgress tolerance to aluminum toxicity into common bean (Butare et al. 2011). Table 1.1 gives an overview on crop wild relatives with confirmed or potential interesting stress tolerance traits.

1.3.3 Tertiary Gene Pool

The tertiary gene pool consists of taxa remotely related to the crop and naturally incapable of interbreeding with the crop, but that can be carried out with specific techniques such as protoplast fusion, embryo rescue or genetic engineering. Such genetic resources are only used if there are major limits for the genetic improvement within the primary and secondary gene pools, for example by introgressing genes for tolerance to abiotic and biotic stress. According to Vincent et al. (2013), here are *P. acutifolius* A. Gray, *P. angustissimus* A. Gray, *P. carteri* Freytag & Debouck, *P.filiformis* Benth., *P. maculatus* Scheele, and *P. parvifolius* Freytag.

The tepary bean *P. acutifolius,* is recognized as having greater heat and drought tolerance than common beans (Federici et al. 1990; Teran and Singh 2002; Acosta-Gallegos et al. 2007) hence, it could be used as a model to increase abiotic stress tolerance in common bead (Rao et al. 2013). Interspecific crosses between common bean and tepary bean have already been used to transfer heat resistance genes (CIAT 2015) and common bacterial blight resistance genes (Thomas and Waines 1984; Parker and Michaels 1986; Singh and Muñoz 1999).Only a small portion of genetic variability in tepary bean has been used for common bean improvement, hence there is still potential for large gains to be made through interspecific gene transfer (Singh 2001).

1.3.4 Artificially Induced/Incorporated Traits/Genes

Genetic engineering is a powerful tool to incorporate genes from sources that are inaccessible through traditional crosses (Svetleva et al. 2003). Several attempts have been made to develop reliable transformation methods for engineering common beans with various traits (Rech al. 2008). Genetic manipulations have been conducted

Table 1.1 Confirmed and potential* use of different species in common bean breeding for abiotic and biotic stress resistance

Trait	Species	References
Drought tolerance	*P. vulgaris* var. *aborigineus* *P. acutifolius*	Blair et al. (2016) Mejía-Jiménez et al. (1994)*
Heat tolerance	*P. acutifolius*	Munoz et al. (2004)*
Cold tolerance	*P. coccineus,* *P. costaricensis* *P. dumosus*	Singh (2001)*
Frost tolerance	*P. angustissimus*	Balasubramanian et al. (2004)*
Soil salinity tolerance	*P. acutifolius*	Munoz et al. (2004)*
Aluminum tolerance	*P. coccineus* *P. coccineus*	De Ron et al (2015) Porch et al. (2013)*
Angular leaf spot resistance	*P. coccineus,* *P. dumosus*	Singh (2001) Mahuku et al. (2003)
Anthracnose resistance	*P. coccineus* *P. dumosus*	Mahuku et al. (2002)
Ascochyta blight resistance	*P. dumosus*	De Ron et al. (2015)
Bean stem maggot resistance	*P. coccineus*	De Ron et al. (2015)
Bean yellow mosaic virus resistance	*P. coccineus*	De Ron et al. (2015)
Bruchid resistance	*P. vulgaris* var. *aborigineus*	Osborn et al. (2003)
Common bacterial blight resistance	*P. acutifolius* *P. coccineus* *P. vulgaris* var. *aborigineus*	Singh (2001) Freytag et al. (1982) Beaver et al. (2012)
Fusarium root rot resistance	*P. coccineus*	Singh (2001)
Fusarium wilt resistance	*P. acutifolius*	Porch et al. (2013)
Web blight resistance	*P. vulgaris* var. *aborigineus*	Beaver et al. (2012)
White mold resistance	*P. coccineus* *P. costaricensis* *P.vulgaris* var. *aborigineus*	Schwartz and Singh (2013) Mkwaila et al. (2011)

with biolistic-mediated method but at low efficiencies (0.03–0.9%) (Russell et al. 1993; Aragao et al. 1996; Vianna et al. 2004). Despite the regulatory approval of the transgenic "Embrapa 5.1" common bean with resistance to the Golden Mosaic Virus (BGMV) in Brazil in 2011 (Aragao et al. Aragao 2014; Balsamo et al. 2015; Souza et al. 2018), no genetically modified common bean has been commercialized to date. There is still a lack of an appropriate and reproducible transformation method for generating stable transgenic common bean plants. The key drawback has been the recalcitrance of common bean genotypes from non-meristem-containing tissues to in vitro regeneration (Veltcheva et al. 2005; Mukeshimana et al. 2013; Solis-Ramose et al. 2019).

1.4 Glimpses on Classical Genetics of and Traditional Breeding for Biotic Stress Resistance

Farmers and breeders had only phenotypic traits before the development of molecularmarkers to choose suitable individuals to interbreed. To assess and select useful genotypes, relatively longperiods of time, many generations and significant economic resources were required. This changed when the use of DNA-based molecularmarkers in breeding programs started in the 1980s (Kole and Gupta 2004). More recently, the advancement of large sequencing technologies has resulted inthe systematic use of thousands of molecular markers. Breeders can now use these high-performance sequencing methods to sequence large populations, research the genetic makeup of crop varieties, understand evolutionary relationships between cultivarsand wild relatives, and possibly provide the basis for modeling complex relationships between genotype and phenotype at the whole-genome level (Cobb et al. 2013; Varshney et al. 2014).

In recent years, new genetic tools, including intraspecific and interspecific mapping populations, molecular and associationmaps, quantitative trait loci (QTL), marker-assisted selection (MAS), and genomic selection (GS), have been created and accumulated. The genome of common beanwill enable a deeper, faster and clearer understanding of its genomic architectureand deliver climate resilient and high nutrition varieties for a sustainable agriculture both from ecological and an economic point of view.

Common beans are grown all over the world under much contrasted conditions, from the humid tropics in Latin America and Africa to the semi-arid highlands of Central America and Mediterranean basin and the High Plains of the US and Canada. In each area there are many production methodsand a unique set of biotic and abiotic constraints. Therefore, the goals of breeding program in common bean must be tailoredto meet the needs of farmers who use the cultivars (Kelly 2001; Santalla et al. 2001; Singh 2001).

Improvement in yields remain themost significant target trait for most common bean breeding programs. Improving yield includes addressing several biotic and

abiotic stresses, using a wide set of techniques, including different germplasms as parents, making several crosses, choosing major gene traits under conditions conducive to selection, and testing a large number of breeding lines. For each growing area and/orgrowing type, these stresses are unique. In most cases, however, fungal diseases are the major biotic stress, along with viruses and insects, while the key abiotic stresses are drought and heat stress at flowering, along with cold, low phosphorus, aluminum toxicity, manganese toxicity, and salinity (Singh 1992; Beebe 2012).

Over the past 40 years, convencional breeding has yielded significant achievementsin common bean. Moderate progress has been made in the production and release ofdry bean cultivars with greater seed yield using traditional plant breeding techniques (Singh 1991; Kellyet al. 1998). Improvement in pods/plant, seed/plant, and seed weight has contributed to the majority of efforts to increase seed yield in favorable environments (Bezaweletaw et al. 2006; Ribeiro et al. 2008). Several studies founded that hybridization of interracial bean varieties increased yield, particularly in crosses between Mesoamerican and Durango or Jalisco races (Beebe 2012). Increasing yield potential has also been achieved through breeding for abiotic stress tolerance. Beebe et al. (2008) stated that through photosynthate remobilization and biomass translocation, yield may increaseunder drought conditions, suggesting that yield improvements can be made under abiotic stress conditions.

Important progress has been made in the production ofresistant cultivars for different diseases using traditional breeding methods.For several disease resistance genes, molecular markers were developed and successfully used to improve common bean cultivars and germplasm (see Sect. 1.6 in this chapter and Table 1.2 for a summary of several important resistance-mapping research).

In response to climate change and increased use of marginal environments for bean production, selection for greater tolerance to abiotic stress such as drought, heat and low soil fertility is expectedto rise significantly. Improved common bean cultivars and breeding lines have been developed with enhanced tolerance to many important abiotic stresses such as drought (Frahm et al. 2004; Muñoz-Perea et al. 2006; Brick et al. 2008), low soil P (Lynch 2007; Beebe et al. 2008), aluminum (Yang et al. 2013), high temperature (Rosas et al. 2000; Beaver et al. 2008), and with improved symbioticnitrogen fixation (SNF) ability (Faridet al. 2017).

In recent years, nutrition and quality traits have become prioritiesfor severalbreedingprograms. Diversity in common bean seed micronutrient concentration (Beebe et al. 2000) and an approach to improving iron and zinc bioavailability for humans have been described. Cooking time (Elia et al. 1997; Cichy et al. 2019) and quality of canner (Hosfield and Uebersax 1980) are two major factors associated with consumer preference of dry beans. The quality of canned bean products can be evaluated on seed coat splitting, seed clumping, broth viscosity, extruded starch, or undesirable seed shape, color or size. Quality can be variable and is impacted by seed quality, canning protocol and genotype (Ghasemlou et al. 2013).

Conventional breeding approaches have allowed the development of many important common beancultivars over the past decades. Recent advances in common bean genomics have enabled greater access to key genomicregions that affect different

Table 1.2 Molecular linkage maps in common bean

Parents	Map size	Markers/traits mapped[a]	References
XR235-1–1/Calima (BC_1)	960	224 RFLPs, 9 seed proteins, 9 isozymes, *P*	Vallejos et al. (1992)
BAT 93/Jalo EEP558 (F_2)	1226	194 RFLP, 24 RAPDs, 15 SSR/ALS, ANT, CBB, *V, C,* Rhizobium	Nodari et al. (1993), Gepts (1999), Yu et al. (2000a)
Corel/Ms8EO2 (BC_1)	567.5	51 RFLP, 100 RAPD, 2 SCAR/ANT	Adam-Blondon et al. (1994)
Midas/G 12,873 (RIL)	1,111	77 RFLPs, 5 isozymes /domestication traits	Koinange et al. (1996)
DOR364/XAN176 (RIL)	930	147 RAPDs, 2 SCARs, 1 ISSR/ASB, BGYMV, CBB, *R*, *V*, *Asp*, rust	Miklas et al. (1998, 20001996)
BAC6/HT7719 (RIL)	545	75 RAPDs/CBB, WB, rust	Jung et al. (1996)
PC50/XAN159 (RIL)	426	168 RAPDs/CBB, *C*, *V*, rust, WM	Jung et al. (1997), Park et al. (2001)
BAT 93/Jalo EEP558 (RIL)	1226	120 RFLP, 430 RAPD, 5 isozymes/BCMV	Freyre et al. (1998)
BelNeb-RR-1 /A55 (RIL)	755	172 RAPDs, 2 SCARs/BBS, HB, BCMV	Ariyarathne et al. (1999), Fourie et al. (2004)
Eagle/Puebla152 (RIL)	825	361 RAPDs/RR	Vallejos et al. (2001)
Jamapa/Calima (RIL)	950	155 RAPDs, 88 RFLPs/RGA	Vallejos et al. (2001)
OACSeaforth/OAC 95–4 (RIL)	1,717	49 AFLPs, 43 RFLPs, 11 SSRs, 9 RAPDs, 1 SCAR/CBB, agronomic traits	Tar'an et al. (2001, 2002)
CDRK/Yolano (RIL)	862	196 AFLPs, 8 RFLP/SY, *C*	Johnson and Gepts (2002)
DOR364/ G19833 (RIL)	1,720	78 SSR, 48 RFLPs, 102 RAPDs, 18 AFLPs	Blair et al. (2003)
ICACer/G24404 (RIL)	869,5	80 SSRs, 1 SCAR/ *C*, *fin*, *st*, agron traits	Blair et al. (2006b)
G14519/G4825 (RIL)	915.4	46 RAPDs, 68 SSRs/seed Fe and Zn concentrations and contents	Blair et al. (2010)
BAT 93/Jalo EEP558 (RIL)	1,545	199 gene-based, 59 core and 17 other markers	Hanai et al. (2010), McConnell et al. (2010)

(continued)

Table 1.2 (continued)

Parents	Map size	Markers/traits mapped[a]	References
DOR364/BAT477 (RIL)	2,041	1,060 (SSR, EST-SSR, BES-SSR, gene-based markers)/SW, Y, DF, DM	Blair et al. (2012), Galeano et al. (2011, 2012)
IAC-UNA/CAL143 (RIL)	1,865.9	198 SSRs, 8 STS-DArT, 3 SCAR/ALS	Oblessuc et al. (2012, 2013)
SEA5/CAL96 (RIL)	1,351	2,122 SNPs/SW, Y	Mukeshimana et al. (2014)
Stampede/Red Hawk (RIL)		7,276 SSRs and SNPs	Schmutz et al. (2014)
Iapar 81/ LP97-28 (RIL) CDRK / Yolano (RIL)	815.9 936	773 SNPs/$SY9^{IL}$ 5,398 SNPs	Elias (2018) Valentini et al. (2018)

[a]ALS: Angular Leaf Spot, BCMV: Bean Common Mosaic Virus, CBB: Common Bacterial Blight, HB: Halo Blight, RR: Root Rot, WM: White Mold, SW: Seed Weight, SY: Seed Yield, DF: Days to Flowering, DM: Days to Maturity, Y: Yield, *fin*: Determinacy, *Ppd*: Gene for Photoperiod Sensitivity, *V*: Flower Color, *C*: Seed Color

biotic and abiotic stress tolerance andgrain yield. Availability of common bean reference genome sequence will be of great importance for addressing the domestication and evolution-related queries and functional dissection of traits of breeding relevance.

Future targets in common bean breeding include (i) increased and equitable access to improved dry bean varieties resistant to multiple environmental and climate change-related stresses; (ii) increased access to micro nutrient rich bean varieties and the adaptation of seed composition to novel end-use application possibilities, and (iii) increased access to high value bean products (varieties) targeted to niche markets.

1.5 Brief on Diversity Analysis

1.5.1 Phenotype-Based Diversity Analysis

Wild forms, landraces, and commercial cultivars from all over the world have been extensively collected and characterized using standardized sets of descriptors (CIAT 1980; IBPGR 1982), which are used to describe accessions and divide them into subgroups due to phenotypic variation (Leakey 1988; see Sect. 1.8 in this chapter). This simplistic phenotypic method has been considered useful in order to understand the extent of genetic variation between accessions.

Major classifications of common beans are based on market classes and agro-morphologic traits (Voysest and Dessert 1991; Santalla et al.2002). Market classes in common bean are mostly characterized by distinctive in pod color, shape, and size as well as seed shape (round, oval, cuboid, kidney, and elongate), seed size (varies from small-medium to large size), seed color (white, cream, yellow, brown, pink,

red, purple, black, and other like gray/green/etc.), seed pattern or striation (striped, mottled, and bi-color) (Singh 2001). Seed also varies in terms of surface texture from shiny (brilliant) to opaque to intermediate. Common bean genotypes can also be grouped according to growth habit into five groups: Type I (determinate bush), Type II (indeterminate bush), Type III (indeterminate semi climber), and Type IV (indeterminate climber), Type V (determinate climber) (Singh 1991). In addition to growth habit, beans are often categorized by origin, primarily by the two Andean and Mesoamerican gene pools and by races within the two gene pools (Singh et al. 1991; Beebe et al. 2013). Compared to the Andean gene pool, the Mesoamerican gene pool is characterized by either small (<25 g 100 seed weight^{-1}) or medium (25–40 g 100 seed weight^{-1}) seeds. In the Andean gene pool, race Nueva Granada includes large-seeded light and dark red kidney, white kidney, bush cranberry, most green beans, and yellow beans, while race Chile includes the vine cranberry bean (Gioia et al. 2019). Within the Mesoamerican gene pool, race Mesoamerica includes the small-seeded black, white and navy beans; while race Durango includes the medium-seeded pinto, great northern, small red, and pink beans (Gioia et al. 2019).

Exploitation of genetic resources in common bean breeding is still limited in comparison to availability of materials, and the potential impact of their use is far from optimal. Hundreds of accessions are conserved and maintained in gene banks with very little information available (i.e., lack of comprehensive information regarding passport data and descriptors useful for users, accession heterogeneity, non-harmonized data, e.g.), making their selection and use for specific purposes by researchers and breeders difficult.

1.5.2 Genotype-Based Diversity Analysis

Various marker systems have been applied to analyze diversity or polymorphisms in common bean but more recently single nucleotide polymorphism (SNP) markers are of interest (Hyten et al. 2010; Felicetti et al. 2012; Blair et al. 2013; Goretti et al. 2014; Zou et al. 2014, see also Sect. 1.6 in this chapter). Expressed sequence tags (ESTs) have been used at the transcriptional level to discover and classify genes differentially expressed under different conditions. Whole genome transcriptome analysis is also an efficient way to exploit key factors involved in transcriptional and metabolic activities for common bean responses to biotic and abiotic stress (Schmutz et al. 2014; Vlasova et al. 2016).The genomics era has resulted in a rapid increase in available sequence data, which can provide a more accurate picture of the genetic diversity and structure of germplasms of crops, along with the identification of genetic variants on the basis of important heritable target traits (Luikart et al. 2018).The current availability of high-throughput sequencing platforms has enabled the release of the high-quality reference genomes of the Andean genotype G19833 (Schmutz et al. 2014) and the Mesoamerican genotype BAT93 (Vlasova et al. 2016). A further high-quality common bean reference genome of race Durango pinto UI111 genotype was recently released (*Phaseolus vulgaris* UI111 v1.1, DOE-JGI and USDA-NIFA, http://

phytozome.jgi.doe.gov/). The assembly of the *P. vulgaris* genome is allowing a better and deeper understanding of its genomic architecture and will serve as an invaluable genomic guide to further develop our molecular-level knowledge of common beans and can be extended to molecular breeding for plants with improved biotic and abiotic tolerance.

1.5.3 Relationship with Other Cultivated Species and Wild Relatives

P. vulgaris exists as wild in South America with further five closely related taxa: *P. coccineus, P. dumosus, P. costaricensis, P. albescens,* and *P. persistentus*, which again relate to a number of other *Phaseolus* species. Wild *P. coccineus*grows wild from Mexico to Guatemala (Nabhan 1985; Debouck et al. 1995), while *P. dumosus* grows wild in western Guatemala and the Northern Andes, often as a weed (Schmit and Debouck 1991). *P. costaricensis* grows in the mountains of Costa Rica and Panama (Freytag et al. 1996; Araya-Villalobos et al. 2001), while *P. albescens* grows in the forests of Mexico (Ramírez-Delgadillo and Delgado-Salinas 1999).

Introgression, especially between cultivated and wild *P. vulgaris* and with *P. coccineus*, occurred in these centers of diversity (Wall 1970).

1.5.4 Relationship with Geographical Distribution

After domestication, crop species have extended their geographical distribution to large areas exploring highly diverse habitats from their relatively small canters of origin located in particular ecological niches. Through the selection of local varieties (i.e. landraces) correlated with adaptation to new and sometimes intense conditions, this process led to crop diversification. Bellucci et al. (2014) found that in common bean a small fraction (2.8%) of the genes detected as domestication outliers resulted in the wild forms fixed (monomorphic), whereas in the domesticated were highly polymorphic. Adaptive processes are expected to be connected to this new functional diversity. Bitocchi et al. (2017), which examined nucleotide sequences at 49 gene fragments on a collection of 45 *P. vulgaris* accessions, mostly wild and domesticated from Mesoamerica, also reported similar findings. Moreover, Bitocchi et al. (2017), in five genes of domesticated forms, detected an increase in functional diversity, and the function of these genes, expressed as plant reaction to biotic and abiotic stresses, suggests that they are involved in adaptation.

The Colombian Exchange that started after the voyage of Columbus 1492 was a major event that facilitated the dissemination of common bean and several other crop species worldwide. This process is very recent in its evolutionary scale (i.e. 400–500 generations for annual crops) and is an important experimental model for

understanding the rapid adaptation of crop plants to evolving environments and dissecting the genomic basis for adaptation to the environment.

Common bean represents an ideal model for these studies as it was rapidly disseminated out of the New World but also due to its two highly differentiated gene pools (Andean and Mesoamerican) that were introduced in different proportion in different continents. In Europe, a higher proportion of Andean genotypes are found (Gepts and Bliss 1988; Lioi 1989a, 1989b; Logozzo et al. 2007; Angioi et al. 2010; Gioia et al. 2013), while Mesoamerican forms are largely present in Argentina (Burle et al. 2010) and China (Zhang et al. 2008) and a balanced proportion of Mesoamerican and Andean types is found in Africa (Gepts and Bliss 1988; Asfaw et al. 2009; Blair et al. 2010). The breakdown of the spatial geographical barriers between the Mesoamerican and Andean types is especially interesting in terms of genetic variability and adaptation. This favored hybridization and recombination between the two gene pools and lead to the occurrence of novel genetic combinations and, consequently, novel genotypic and phenotypic variation (Angioi et al. 2010; Gioia et al. 2013), which again has been a key tool for breeding programs aimed to develop novel varieties. Evidence of this phenomenon has been detected using phaseolins, allozymes, and morphological data (Santalla et al. 2002; Rodiño et al. 2006), as well as inter-simple sequence repeats (ISSRs) and simple sequence repeats (SSRs) data from both the chloroplast and nuclear genomes (Sicard et al. 2005; Angioi et al. 2010; Gioia et al. 2013). Gene flow between both gene pools appears to be relatively common in the Andean (Debouck et al. 1989; Beebe et al. 1997; Chacón et al. 2005) and European zones (Santalla et al. 2002; Sicard et al. 2005; Angioi et al. 2010; Gioia et al. 2013).

1.5.5 Extent of Genetic Diversity

Modern varieties of common bean are inbred but wild plants, and to some extent landraces, have proportion of outcrossing. Landraces are therefore usually more diverse than modern varieties, and landraces often comprise of a mixture of more or less homozygous lines (Fig. 1.2) (Pierson 2012). Therefore, such varieties are population varieties, often with a high within-population diversity. Number of plants used in diversity studies is therefore of importance, and for genebanks, regeneration

Fig. 1.2 Photo of the landrace 'Götlandsböna' (NGB11554), collected on the Swedish island Gotland and that include at least two distinct lines (Photo S.Ø. Solberg)

a high number of plants applies for maintaining this diversity (FAO 2014). The extent of genetic diversity is developed further in Sects. 1.7 and 1.8.

1.6 Molecular Mapping of Resistance Genes and QTLs

1.6.1 Brief History of Mapping Efforts

Genetic linkage maps are useful tools for genetic analysis and have played a major role in genetic common bean improvement. They have been extensively used for many genetic applications such as tagging genes of interest to facilitate marker assisted selection (MAS) programs, cloning of agronomically important genes, comparative mapping, and analysis of germplasm diversity (Gepts 1999; González et al. 2017). In the literature, several common bean linkage maps have been reported (Table 1.2), and they include different features such as the types of parents and segregating population used, the type of markers and traits segregating in each population, the total map length, and the degree of saturation of the genome. The first common bean linkage maps were developed using markers with low-throughput markers, which resulted in low density maps. In this context, an international consortium called 'Phaseomics' and the BeanCAP project (USDA Common Bean Coordinated Agricultural Project) were developed to establish the necessary framework of knowledge and materials for the advancement of bean genomics, transcriptomics, and proteomics (Gepts et al. 2008; Fonsêca et al. 2010; Hyten et al. 2010). As a result, genotyping technologies and high-throughput molecular marker technology have contributed to produce high density maps enabling high precision QTL mapping (or high-density functional maps) and will accelerate MAS and genomic-assisted breeding (GAB) in common bean.

1.6.2 Marker Types

The first genetic common bean linkage map was based on morphological markers and showed a reduced genomic coverage (Lamprecht 1961). Later, it was further extended with seed proteins and isozymes (Bassett 1988; Koenig et al. 1990; Vallejos and Chase 1991) providing the baseline for the development of the DNA-based linkage maps.

There was a parallel evolution of common bean genetic maps and the development of molecular marker technologies. Moreover, molecular markers allowed to increase to a great extent the number of polymorphic loci in the mapping populations. Initially, linkage maps were developed based on DNA hybridization markers like restriction fragment length polymorphism (RFLP) which allowed the development of the first DNA-based genetic maps in common bean due to their great robustness and repeatability (Vallejos et al. 1992; Nodari et al. 1993). These maps were subsequently used to

compare and integrate different genetic maps (Adam-Blondon et al. 1994; Koinange et al. 1996; Freyre et al. 1998; Gepts 1999; Yu et al. 2000b). With the development of the PCR, new molecular markers were used for genetic mapping, among which random amplified polymorphic DNA (RAPD) (Williams et al. 1990), amplified fragments length polymorphism (AFLP) (Vos et al. 1995), simple sequence repeats (SSR) (Tautz 1989), and inter-simple sequence repeat (ISSR) (Zietkiewicz et al. 1994) have been the most applied. PCR-based molecular markers were used for saturating the RFLP maps and to create new ones based on additional mapping populations (Freyre et al. 1998; Ariyarathne et al. 1999; Yu et al. 2000b; Blair et al. 2003, 2010; Fourie et al. 2004).

The first RFLP-based genetic map, constructed using 224 RFLP marker loci, nine seed proteins, nine isozyme markers and the seed and flower color marker *P*, was developed by Vallejos et al. (1992). These markers were distributed into 11 linkage groups (LGs) covering 960 cM of the common bean genome. A second RFLP-based genetic map included 108 RFLPs, seven RAPDs, seven isozymes and 18 loci corresponding to 15 known genes, the *I* gene for bean common mosaic virus (BCMV) resistance, a seed color pattern gene, and a flower color gene (Nodari et al. 1993). All these markers were grouped into 15 LGs, with an average interval of 6.5 cM between markers, covering 827 cM of the bean genome. This map was later improved by Gepts et al. (1993) which included 204 markers grouped into 13 LGs covering 1060 cM. Adam-Blondon et al. (1994) constructed a third map including 157 markers: 51 RFLPs, 2 SCARs (sequence characterized amplified regions), 100 RAPDs and four morphological markers, spanning 567.5 cM of the bean genome. A preliminary correspondence with the map developed by Vallejos et al. (1992) was established by Adam-Blondon et al. (1994) since 19 RFLP markers were shared between both maps. The first core linkage map of common bean was constructed by Freyre et al. (1998) on the base of the shared RFLP markers among these three previous maps (Vallejos et al. 1992; Nodari et al. 1993; Adam-Blondon et al. 1994). This map included 563 markers: 120 RFLPs and 430 RAPDs, in addition to a few isozyme and phenotypic marker loci, which were sorted into 11 LGs covering 1226 cM.

In successive years, SSR markers, which are highly polymorphic PCR-based markers, replaced RFLP markers to anchor different genetic maps. The first successful assignment of 15 SSRs to a framework map based on RAPD and RFLP markers was published by Yu et al. (2000b). With the availability of EST (expressed sequence tag) sequencing programs several functional markers have been developed from coding genomic regions. Blair and collaborators in 2003 were the first to incorporate SSR markers developed from EST databases in a linkage map, which comprised a total of 246 loci (78 SSR, 48 RFLP, 102 RAPD and 18 AFLP markers) covering 1720 cM. In successive years, EST libraries become an important source of gene-based markers, like EST-SSR, single nucleotide polymorphism (SNP) and insertion/deletion (InDel), which are valuable markers representing transcribed sequences that can be associated with phenotypic characteristics (Hanai et al. 2010; Galeano et al. 2012; Oblessuc et al. 2012). Since then, functional markers have been progressively incorporated in the common bean linkage maps. Furthermore, functional maps allowed synteny comparisons between the common bean and other

genomes since EST based markers are highly conserved between species (McConnell et al. 2010).

With the advent of the next-generation sequencing (NGS) technology, high-throughput genotyping approaches were developed allowing the rapid and cost-effective generation of high-density functional maps. In this way, a SNP resource developed by the USDA BeanCAP project, the Illumina Infinium assay BARCBean6K_3 BeadChip resulted a valuable tool for high-throughput genotyping leading to the direct gene tagging for QTL mapping of different common bean resistance loci by using standard bi-parental populations or association panels (Brisco et al. 2014; Miklas et al. 2014; Hagerty et al. 2015;Viteri et al. 2015;Nakedde et al. 2016; Zuiderveen et al. 2016).

Moreover, with NGS technology sequencing of complete plant genomes has become increasingly more accessible and routine. Nowadays, the whole genome of common bean has been sequenced and the complete genomes of the Mesoamerican and Andean beans BAT93 and G19833 are available (Schmutz et al. 2014; Vlasova et al. 2016). Moreover, the PhaseolusGenes database, (http://www.beancap.org/; http://phaseolusgenes.bioinformatics.ucdavis.edu/), developed as part of the BeanCAP project resulted a useful tool to place markers on assembled common bean and soybean genomes. The whole genome sequence accelerates the development of markers for high throughput genotyping to be used in plant breeding and genetic studies promoting the identification of makers tightly linked to agronomical important traits (Moghaddam et al. 2014; Meziadi et al. 2016; Valentini et al. 2017).

1.6.3 Mapping Populations Used

In common bean genetic mapping, several segregating populations have been used (Table 1.2). As common bean breeding programs have different economic traits of interest, widely divergent parents were chosen to maximize the genetic polymorphism at the nucleotide level, the phenotypic variation and variability for disease resistance and other traits. Also, in many cases, the parents were chosen to belong to different gene pools because in this way the polymorphism among genotypes was markedly increased (Nodari et al. 1992; Haley et al. 1994). For instance, to develop the first linkage map, Vallejos et al. (1992) used a mapping population which consisted of a backcross progeny (BC_1) between the Mesoamerican line XR-235–1-1 with the Andean cultivar Calima (XC). In another study, Adam-Blondon et al. (1994) used a BC_1 population derived from an inter-gene pool cross between two European bean genotypes: Ms8EO2 and Corel (MsCo), whereas Nodari et al. (1993) used a F_2 population derived from the cross between the Mesoamerican line BAT 93 with the Andean cultivar Jalo EEP558 (BJ).

Recombinant inbred line populations (RIL; F_2-derived lines) have been extensively used in common bean mapping (Table 1.2). For example, the BJ F_2 mapping population was advanced to a RIL to develop the first core linkage map of common bean (Freyre et al. 1998), and then was later improved by McConnell et al. (2010)

and Hanai et al. (2010). Furthermore, the base map developed by Blair et al (2003) using SSR markers was performed using a RIL derived from the cross between the Mesoamerican variety DOR364 and the Andean landrace G19833 (DG). Likewise, numerous RIL populations were developed and used for bean genetic mapping studies and QTL identification in the last years (Blair et al. 2006b, 2010; Hanai et al. 2010; Oblessuc et al. 2012). For genetic mapping studies, the RIL populations derived from the BJ and DG inter-gene pool crosses have been broadly used since they are considered core mapping populations (Freyre et al. 1998; Blair et al. 2003, 2006a; Galeano et al. 2009, 2011, 2012; McConnell et al. 2010; Hanai et al. 2010).

1.6.4 Mapping Software Used

A genetic map is a list of genetic elements ordered according to their co-segregation patterns. Genetic maps of plants species whose genomes are yet to be sequenced provide an essential resource to understand the order and spacing of markers, and to leverage additional genetic information through comparative mapping with genetic maps and genome sequences of other plant species. Further, genetic maps allow studies of plant genes implicated in key plant traits (Cheema and Dicks 2009). In species whose genomes have been sequenced, genetic maps provide a scaffold for genome sequence assembly and validation, and they enable the suggestion of candidate genes conditioning any specific trait. Additionally, genetic maps can be used for marker-assisted selection in breeding programs (Cheema and Dicks 2009). Mapmaker is used to construct linkage maps, developed by Lander et al. (1987), using an algorithm for the simultaneous multipoint analysis of various loci. Polymorphic marker loci are essential to obtaining genetic linkage maps, and the advent of restriction fragment length polymorphism (RFLP) first allowed such genetic studies. Linkage analysis uses the maximum likelihood to construct genetic linkage maps from F_2 intercrosses, or from two- and three-generation nuclear families in natural populations (Lander et al. 1987). With the emergence of advanced genomic sequencing technologies, genotyping becomes easier and faster, frequently using SSR, SNP, and KASP markers to construct linkage maps.

JoinMap was developed by Stam in 1993 and comes with the differential of construct genetic maps with linkage data collected in different experiments. It performs a sequential build-up of the map and, at each step, a numerical search for the best fitting order of the markers, wherein the distance is estimated by weighted least square. Building an integrated map is necessary to determine marker positions segregating only one parent relative to another, and the linkage analysis of experiments based on inbred line crosses is less complicated than for other crosses (Van Ooijen 2011). Most plant model species and many important crop species are autogamous, which has propitiated linkage analysis for species inbreeding. Molecular markers, such as Single-Nucleotide Polymorphisms (SNPs), are now widely used for constructing linkage maps in all major crops.

A genetic linkage map of the common bean based entirely on SNPs is useful for identifying genes/QTL-controlling traits and marker-assisted selection. High-density common bean linkage maps containing thousands of SNP markers were constructed by Song et al. (2015). These SNPs were identified by aligning millions of reads to the Andean reference sequence (G19833) of the common bean (Schmutz et al. 2014). For this purpose, a total of 110 RILs from the mapping population California Dark Red Kidney (Andean) × Yolano (Mesoamerican) were used in this study. The development of the CY population was described by Johnson and Gepts (1999, 2002).

Seeds of each line were multiplied at the greenhouse of the Universidade Estadual de Maringá, Paraná, Brazil. Leaf tissue harvested from single plantlets and high-quality genomic DNA for SNP genotyping was isolated with the PureLink® Genomic DNA Mini Kit, following the manufacturer's instructions. The 110 CY RILs and parents were screened with 5,398 SNP markers of the Illumina BeadChip BARCBEAN6K_3 (Song et al. 2015), following the Infinium HD Assay Ultra protocol (Illumina, Inc., San Diego, CA). The fluorescence intensity obtained by the BeadChip was visualized using Illumina BeadArray Reader. SNP alleles were automatically called using Illumina GenomeStudio V2011.1 (Illumina, Inc., San Diego, CA). Allele calls were visually inspected and errors in allele calling were manually corrected. Molecular analysis was performed at the USDA-ARS Soybean Genomic and Improvement Laboratory in Beltsville, MD. For linkage map construction, a pre-selection of SNPs was carried out in Microsoft Excel. Distances between markers were calculated using Kosambi's mapping function with default parameters in JoinMap 4.1.

1.6.5 Details of Genetic Linkage Maps

Song and collaborators in 2015 studied the mapping population of 267 F_2 plants derived from the Stampede × Red Hawk common bean cross developed by Dr. Phil McClean at North Dakota State University. Linkage maps were constructed using JoinMap 4.0 (Van Ooijen 2006). As a result, the 267 F_2 plants of the Stampede × Red Hawk population were genotyped with the BARCBean6K_1 and BARCBean6K_2 BeadChips. After elimination of SNPs with missing data >10%, or loci with significant segregation distortion from a 1:2:1 ratio as measured by $\chi 2$ at the 1% significant level, 6,531 SNPs were retained for linkage analysis. Analysis of 7,040 markers, including 25 framework markers and 484 previously mapped SNPs, produced a genetic map consisting of 11 consensus linkage groups that spanned 1042.2 cM of Kosambi map distance. The average number of markers mapped per linkage group was 640, ranging from 225 to 979.

Previous studies performed the co-segregation analysis of resistance to *C. lindemuthianum* races 7 and 73 and *P. griseola* race 63–39 in a Ouro Negro cultivar using an F_2 population from the Rudá × Ouro Negro cross and $F_{2:3}$ families from the AND 277 × Ouro Negro cross. Results from Gonçalves-Vidigal et al. (2013) revealed that the ANT resistance gene *Co-3*^{4} and the ALS resistance gene *Phg-3* co-segregated

and were tightly linked to marker g2303 at a distance of 0.0 cM on Pv04 (Fig. 1.3). The close linkage between the *Co-3*^{4} and *Phg-3* genes and prior evidence is consistent with the existence of a resistance gene cluster at the end of chromosome Pv04, which contains the ANT resistance QTL *ANT4.1*^{UC} in addition to *Co-3*^{4} and *Phg-3* (Oblessuc et al. 2014).

Studies conducted by Valentini and collaborators in 2018 resulted in a common bean high-density SNP map using a California Dark Red Kidney (CDRK) × Yolano (CY population) RIL population. A total of 110 CY lines and parents CDRK and Yolano were screened with 5,398 SNP markers of the Illumina BeadChip BARCBEAN6K_3 following the Infinium HD Assay Ultra protocol (Illumina, Inc., San Diego, CA). After elimination of SNPs with a high frequency of missing data, or loci with a minor allele frequency of 30%, 3,277 SNP markers were selected to participate in linkage mapping analysis. Distances between markers were calculated using Kosambi's mapping function with default parameters in JoinMap 4.1.

The final linkage map for the population CDRK × Yolano, comprising 11 consensus linkage groups, spanned 936 cM with an average interval of 0.3 cM between markers (Table 1.3). The average number of markers mapped per linkage group was 290, ranging from 160 to 406. This map covered 512.15 Mbp of the genome, based on the physical distance (bp) between the first and last SNPs mapped to each chromosome. The average recombination rate (Kb/cM), measured by the physical (Kb) and genetic (cM) position of the last marker mapped in each chromosome, was 565.7 Kb, like an earlier observation around the Phaseolin locus. The

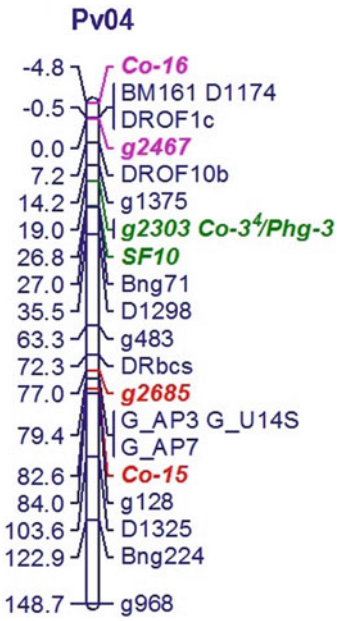


Fig. 1.3 Genetic distances and locations of the *Co-3*^{4} gene for resistance to common bean ANT, the *Phg-3* gene for resistance to ALS, and the molecular markers g2303 on linkage group Pv04 of *Phaseolus vulgaris* L. Map drawn with MapChart (Voorrips 2002; Gonçalves-Vidigal et al. 2013)

Table 1.3 Linkage group, number of SNPs, genetic and physical length, and recombination rate (Kb/cM) per chromosome for the RIL population CDRK × Yolano. Physical length (Kb) is based on the physical distance (bp) between the first and last SNPs mapped to each chromosome

Linkage group	Number of SNPs	Genetic length (cM)	Physical length (Kb)	Kb/cM
Pv01	328	90.17	51,870.7	575.3
Pv02	365	111.38	49,027.0	440.2
Pv03	264	116.82	52,103.9	446.0
Pv04	290	83.73	45,759.9	546.5
Pv05	406	90.22	40,452.9	448.4
Pv06	208	56.49	31,957.2	565.7
Pv07	332	90.47	51,531.0	569.6
Pv08	369	85.43	59,494.1	696.4
Pv09	285	90.61	37,039.7	408.8
Pv10	270	55.83	42,724.4	765.3
Pv11	160	65.23	50,187.1	769.4
Total	3,277	936.38	512,147.9	–
Mean	290	90.17	49,027.0	565.7

genetic position of most SNPs in the linkage maps was consistent with the physical positions along each chromosome of the *Phaseolus vulgaris* genome assembly V1.0 (Fig. 1.4). Additionally, the genetic and physical distances for the 3,277 SNPs mapped using the CY RIL population were correlated with the observed distances reported by Song et al. (2015).

To determine the genetic basis of disease resistance in the genotype CDRK, 110 RILs derived from the California Dark Red Kidney × Yolano (CY) RIL population described by Johnson and Gepts (1999) were used. SNP markers that were polymorphic between the parents CDRK and Yolano segregated at a 1:1 ratio in the RIL population, as measured by the $\chi 2$ test at $p = 0.01$, were used to create a linkage map using the default settings of JoinMap 4.1 (Van Ooijen 2006). Briefly, the regression-mapping algorithm based on the Kosambi map function was used to define the linkage order and genetic distances in centiMorgans (cM). A minimum likelihood of odds (LOD) ≥ 3.0 and a maximum distance of $\leq$50 cM were used to test linkages among markers. A genetic linkage map was created using MapChart (Voorrips 2002). SNP markers flanking the genomic locations associated with ANT and ALS disease reactions were used to define the physical region of these loci based on the bean reference genome v.1.0 (Schmutz et al. 2014), available in NCBI v.1.0 (http://phytozome.jgi.doe.gov).

Genetic linkage analysis conducted between the $CoPv01^{CDRK}$/$PhgPv01^{CDRK}$ loci and SNPs showing the expected segregation of 1:1 in the RIL population revealed that loci are flanked by the SNP markers ss715645251 and ss715645248 (Fig. 1.5) in a genomic region on chromosome Pv01 (Gonçalves-Vidigal et al. 2020). Based on the bean reference genome v1.0 (https://www.ncbi.nlm.nih.gov), these markers

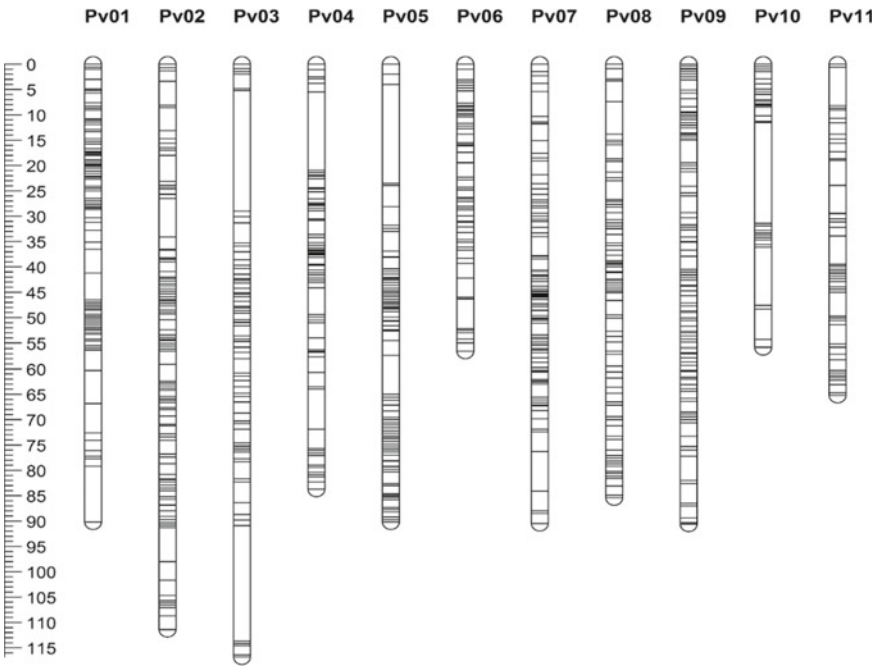


Fig. 1.4 Genetic mapping of the RIL population CDRK × Yolano using 3,277 SNP markers assigned to the 11 linkage groups of common bean. Scale in centiMorgan (cM) distance indicated on the left side. Distances between markers were calculated using Kosambi's mapping function with default parameters in JoinMap 4.0 (Van Ooijen 2006). Genetic linkage maps were designed using MapChart (Voorrips 2002; Valentini et al. 2018)

are located at positions of 50,301,532 bp and 50,546,985 bp, respectively, which correspond to a distance of 245.6 Kb.

A fine linkage map was developed with 17 SNPs, two additional SSRs (BARCPVSSR01358 and BARCPVSSR01361), and the STS CV542014 markers (http://phaseolusgenes.bioinformatics.ucdavis.edu/markers/1009). To reduce the distance between SNP markers ss715645251 and ss715645248 markers in the genomic region containing the $CoPv01^{CDRK}$/$PhgPv01^{CDRK}$ loci, Gonçalves-Vidigal et al. (2020) performed a fine-mapping analysis by genotyping 19 RILs that showed recombination events in the 245.6 Kb region. Recombination events were identified based on the genotypic data of all 110 RILs obtained with the BARCBEAN6K_3 BeadChip.

Upon genotyping these 19 RILs with 12 SNPs, two SSRs, and one STS marker, we observed that the susceptible CY5 RIL and the resistant CY48 RIL contained recombination events (Table 1.4) that allowed us to delimit the $CoPv01^{CDRK}$/$PhgPv01^{CDRK}$ loci region to the area between the CV542014 and ss715645248 markers. Based on the bean reference genome (Schmutz et al. 2014) these new $CoPv01^{CDRK}$/$PhgPv01^{CDRK}$ loci flanking markers are located at positions

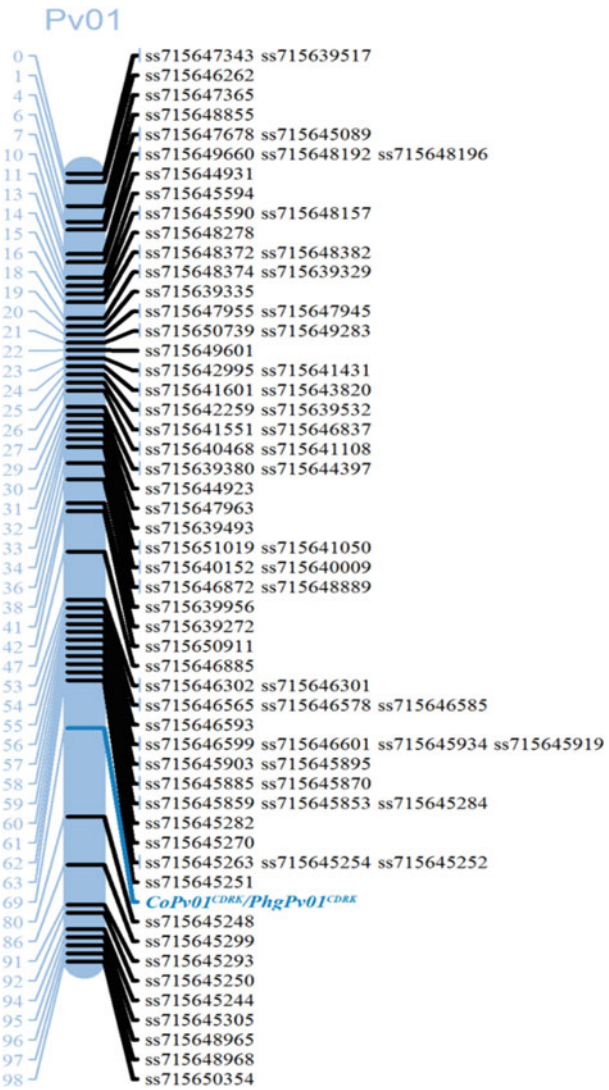


Fig. 1.5 Genetic map of common bean linkage group Pv01 containing the anthracnose and angular leaf spot resistance loci and linked single nucleotide polymorphism (SNPs) markers used to genotype the F_{10} population California Dark Red Kidney × Yolano. Recombination distances are indicated on the left side of the linkage group in centiMorgans (cM), and the marker names are shown on the right side. The *CoPv01*^{CDRK}/*PhgPv01*^{CDRK} resistance loci were flanked by SNP markers ss715645251 and ss715645248 in F_{10} mapping population. The map was drawn with MapChart (Voorrips 2002; Gonçalves-Vidigal et al. 2020)

Table 1.4 Genotype and phenotype of 19 F_{10} recombinant events in the region of Pv01 used for fine mapping of the ANT and ALS resistance loci in CDRK. Genotyping was achieved using flanking markers—12 SNP, two SSR, and one STS—that positioned *CoPv01*^{CDRK}/*PhgPv01*^{CDRK} *l*oci in a 33 kb genomic region flanked by markers CV542014 and ss715645248

Marker	SNP position	Recombinant lines from CDRK × Yolano																		
		5	12	19	20	33	38	43	47	48	62	70	73	79	87	88	91	115	96	146
ss715645260	50115685	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	AA	BB	BB	AA	BB	AB	AB
ss715645259	50130201	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	AA	BB	BB	AA	BB	AB	AB
ss715645258	50155987	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	AA	BB	BB	AA	BB	AB	AB
ss715645257	50161526	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	AA	BB	BB	AA	BB	AB	AB
ss715645256	50182775	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	AA	BB	BB	AA	BB	AB	AB
ss715645254	50203547	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	AA	BB	BB	AA	BB	AB	AB
ss715645252	50222584	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	AA	BB	BB	AA	BB	AB	AB
ss715645251	50301592	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	BB	BB	BB	AA	BB	AB	AB
BARCPVSSR01358	50350345	AA	AA	BB	BB	AA	BB	-	AA	AA	BB	AA	AA	BB	BB	BB	AA	BB	BB	AA
BARCPVSSR01361	50388017	AA	AA	BB	BB	AA	BB	-	AA	AA	BB	AA	AA	BB	BB	BB	AA	BB	BB	AA
CV542014	**50513853**	AA	AA	BB	BB	AA	BB	AA	AA	AA	BB	AA	AA	BB	BB	BB	AA	BB	AB	AB
CoPv01^{CDRK}/*PhgPv01*^{CDRK}		**BB**	**AA**	**BB**	**BB**	**AA**	**BB**	**AA**	**AA**	**AA**	**BB**	**AA**	**AA**	**BB**	**BB**	**BB**	**AA**	**BB**	**BB**	**AA**
ss715645248	**50546985**	BB	AA	BB	BB	AA	BB	AA	AA	BB	BB	AA	AA	BB	BB	BB	AA	BB	AB	AB
ss715645299	51353193	BB	BB	AA	BB	AA	AA	AA	BB	BB	BB	BB	BB	BB	BB	BB	BB	AA	AB	AA
ss715645293	51617802	BB	BB	AA	AA	BB	AA	BB	BB	BB	AA	AA	BB	BB	AA	AA	BB	AA	AA	AA
ss715645250	51726047	BB	BB	AA	AA	BB	AA	BB	BB	BB	AA	AA	BB	BB	AA	AA	BB	AA	BB	AA
ss715645244	51764167	AA	BB	AA	AA	BB	AA	BB	BB	BB	AA	AA	BB	BB	AA	AA	BB	AA	BB	AA
ss715645305	51786948	AA	BB	AA	AA	BB	AA	BB	BB	BB	AA	AA	BB	BB	AA	AA	BB	AA	BB	AA
ss715645301	51819821	AA	BB	AA	AA	BB	AA	BB	BB	BB	AA	AA	BB	BB	AA	AA	BB	AA	BB	AA
ss715648967	51883712	AA	BB	AA	AA	BB	AA	BB	BB	BB	AA	AA	BB	BB	AA	AA	BB	AA	BB	AA
ss715648965	51896315	AA	BB	AA	AA	BB	AA	BB	BB	BB	AA	AA	BB	BB	AA	AA	BB	AA	BB	AA

AA = Resistant; BB = Susceptible; AB = Heterozygous; - = not available.

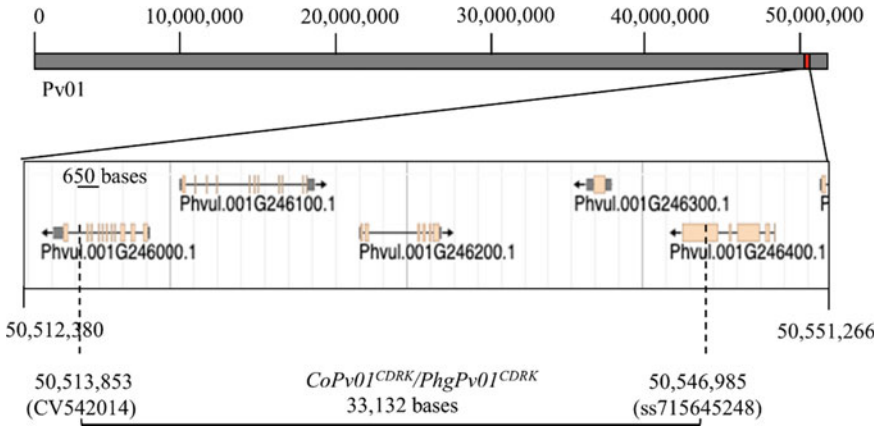


Fig. 1.6 Fine mapped region for the CDRK resistance loci*CoPv01*^{CDRK}/*PhgPv01*^{CDRK}. The upper bar represents the entire chromosome Pv01, with the *CoPv01*^{CDRK}/*PhgPv01*^{CDRK} region highlighted in red. The five predicted genes in this region are shown, with the *CoPv01*^{CDRK}/*PhgPv01*^{CDRK} flanking markers CV542014 and ss715645248 indicated by dashed lines, within the predicted genes Phvul.001G246000 and Phvul.001G246400, respectively. The genomic region between these markers is indicated by the lower bar and covers around 33 Kbp of the genome (Gonçalves-Vidigal et al. 2020)

50,513,853 bp (CV542014) and 50,546,985 bp (ss715645248) of chromosome Pv01, spanning 33 Kb (Fig. 1.6).

1.6.6 Enumeration of Mapping of Resistance Genes and QTLs

1.6.6.1 Disease Resistance

Fungal Diseases

Resistance to anthracnose (ANT), caused by *Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara, is conferred by independently segregating individual loci in a series named *Co* and mapped to date (Table 5). Several of these anthracnose-resistance genes are in clusters, where they are tightly linked to other resistance genes (for angular leaf spot, rust, etc.), and these clusters are often positioned at the ends of chromosomes (Vaz Bisneta and Gonçalves-Vidigal 2020). Currently, the known *Co* genes are *Co-1* and its alleles, *Co-Pa*, *Co-x*, *Co-w*, *CoPv01*^{CDRK}, and *Co-AC* on chromosome Pv01 (Geffroy et al. 2008; Mahiya-Farooq et al. 2019; Gonçalves-Vidigal et al. 2011; Richard et al. 2014; Chen et al. 2017; Lima Castro et al. 2017; Gonçalves-Vidigal et al. 2020; Gilio et al. 2020); *Co-u* and *CoPv02* on chromosome Pv02 (Campa et al. 2014; Geffroy et al. 2008); *Co-13* and *Co-17* on chromosome

Pv03 (Lacanallo and Gonçalves-Vidigal 2015; Trabanco et al. 2015); *Co-3*, *Co-3*^{2}, *Co-3*^{3}, *Co-3*^{4}*/Phg-3*, *Co-y*, *Co-z*, and *Co-RVI* on chromosome Pv04 (David et al. 2008; Gonçalves-Vidigal et al. 2013; Murube et al. 2019); *Co-5*, *Co-6* and *Co-v* on chromosome Pv07 (Young et al. 1998; Geffroy et al. 2008; Sousa et al. 2014); and *Co-2* on chromosome Pv11 (Kelly and Young 1996; Meziadi et al. 2016). Additionally, recent studies conducted by Azevedo et al. (2018) have revealed that COK-4, a putative kinase encoded in the ANT resistance locus *Co-4* that is transcriptionally regulated during the immune response, is highly like the kinase domain of FERONIA (FER) in *Arabidopsis thaliana,* a factor that has a role in balancing distinct signals to regulate growth and defense.

Several sources of resistance to angular leaf spot (ALS), which is caused by the fungus *Pseudocercospora griseola,* (Sacc.) Crous and Braun, have been identified in common bean. Furthermore, single, dominant resistance loci, as well as QTLs conferring resistance to ALS, have been reported (Miklas et al. 2006; Mahuku et al. 2009; 2011; Gonçalves-Vidigal et al. 2011; 2013; Oblessuc et al. 2013; Keller et al. 2015). The genes conferring resistance to ALS formally accepted by the Bean Improvement Cooperative (BIC) Genetic Committee are presented in Table 5. The *Phg-1* on chromosome Pv01 is tightly linked (0.0 cM) to the ANT locus *Co-1*^{4} in cultivar AND 277, which led to the designation of the locus as *Co-1*^{4}*/Phg-1* (Gonçalves-Vidigal et al. 2011). The *Phg-1* locus was discovered using F_2 plants from crosses of AND 277 × Rudá and AND 277 × Ouro Negro inoculated with *P. griseola* race 63–23.

A previous study conducted by de Carvalho et al. (1998) used the name *Phg-1* before describing a resistance locus in AND 277 crossed with Rudá. The molecular marker CV542014^{450} have been found to be linked with the *Co-1*^{4}*/Phg-1* loci at 0.7 cM (Gonçalves-Vidigal et al. 2011). The ALS resistance gene *Phg-2* in Mesoamerican cultivar Mexico 54 was discovered using a cross between Mexico 54 × Rudá and *P. griseola* race 63–19. The authors identified RAPD markers OPN02^{890}, OPAC14^{2400}, and OPE04^{650} as being linked to *Phg-2* at 5.9, 6.6, and 11.8 cM, respectively, on chromosome Pv08. Similarly, the RAPD marker OPE04 was found in all resistant individuals but was absent in those scored as susceptible based on virulence data (Namayanja et al. 2006). Additionally, an allelism test between Mexico 54 and BAT 332 inoculated with *P. griseola* race 63–39 showed that a single, dominant gene controls ALS resistance, suggesting that the resistance to ALS in Mexico 54 and BAT 332 is conditioned by the same resistance locus (Namayanja et al. 2006).

The *Phg*-2^2 allele of BAT 332 is the only allele officially accepted by the BIC Genetics Committee. *Phg-3* has initially been published as *Phg-ON* in cultivar Ouro Negro. This cultivar is an essential of resistance for ALS and other diseases in common bean, such as ANT and rust. Inheritance studies in an F_2 population derived from the Ouro Negro × US Pinto 111 cross revealed one dominant resistance gene conferring resistance to race. To investigate associations between *Co-3*^{4} and the *Phg-3* genes, Gonçalves-Vidigal et al. (2013) conducted a co-segregation analysis of resistance to *C. lindemuthianum* races 7 and 73 and *P. griseola* race 63–39 in Ouro Negro using an F_2 population from the Rudá × Ouro Negro cross and $F_{2:3}$ families from the AND 277 × Ouro Negro cross. This co-segregation analysis showed that *Co-3*^{4} and *Phg-3* are inherited together. Additionally, the genes *Phg-3* and *Co-3*^{4} were

found to be tightly linked to marker g2303 at a distance of 0.0 cM (Gonçalves-Vidigal et al. 2013) on chromosome Pv04.

Furthermore, seven QTLs on five LGs have been reported by Oblessuc et al. (2012). Among these, the major QTL *ALS4.1*^{GS,UD} on Pv04 and *ALS10.1*^{DG,UC} and *ALS10.1*$^{DG,UC,\ GS}$ on Pv10, identified in G5686 and CAL143 (Mahuku et al. 2009; Oblessuc et al. 2012; Keller et al. 2015), have been recently named as *Phg-4* and *Phg-5* (Souza et al. 2016). The *Phg-4* locus was first discovered by evaluating the G5686 × Sprite F_2 population with race 31–0 and was published as *Phg*$_{G5686A}$ (Mahuku et al. 2009). This QTL was later fine mapped to a 418-kb region on chromosome Pv04 and named *ALS4.1*^{GS,UC} (Keller et al. 2015). As this major locus had consistent and significant effects across different environments and populations (Mahuku et al. 2009; Oblessuc et al. 2012, 2013; Keller et al. 2015), the BIC genetics committee accepted the name QTL *ALS4.1*^{GS,UC} for *Phg-4* in G5686 (Souza et al. 2016). The resistance *Phg-5* locus on chromosome Pv10 was discovered using the CAL 143 × IAC-UNA RIL population. The RILs were evaluated under natural infection in the field and in the greenhouse inoculated with race 0–39, whereby QTL *ALS10.1* exhibited a strong effect in all environments (Oblessuc et al. 2012). Keller et al. (2015) confirmed the QTL *ALS10.1* in G5686. Because of its strong effect on resistance to ALS in different environments, the BIC Genetics Committee proposed officially named *Phg-5 ALS10.1* in both G5686 and CAL143 (Souza et al. 2016).

Correspondingly, several genes conferring race-specific resistance to the rust pathogen *Uromyces appendiculatus* (Pers.) Unger has been identified, named, and mapped in different LGs in the common bean genome (Table 1.6). Indeed, three large clusters harboring many resistance genes located at the ends of chromosomes have been identified on Pv04, Pv10, and Pv11 of the *Phaseolus vulgaris* genome (Schmutz et al. 2014). Among these, one of the most complex disease-resistance clusters containing many genes that confer resistance to various common bean pathogens has been identified at the end of the short arm of chromosome Pv04 (Geffroy et al. 2009; Richard et al. 2014). Moreover, 10 major rust resistance genes have been named and mapped in six different LGs of the common bean genome Pv01, Pv04, Pv06, Pv07, Pv08, and Pv11 (Kelly et al. 1996, Miklas et al. 2002; Miklas et al. 2006a; Hurtado-Gonzales et al. 2017). Mesoamerican rust resistance genes include *Ur-3*, *Ur-5*, *Ur- 7*, *Ur-11* and *Ur-14* (Stavely 1984, 1990; Souza et al. 2011). Andean rust resistance genes include *Ur-4*, *Ur-6*, *Ur-9*, *Ur-12,* and *Ur-13*. Besides, several genes conferring resistance to various common bean pathogens are arranged in clusters of tightly linked genes, often located at the end of the chromosomes. For example, *Ur-9* (Pv01), *Ur-5* (Pv04), and *Ur-3* (Pv11) co-localize with ANT resistance genes *Co-1* (Pv01), *Co3* (Pv04) and *Co-2* (Pv11), respectively (Kelly et al. 2003; Geffroy et al. 1999, 2000). Similarly, *Ur-13* maps close to the *Phg-2* gene for ALS resistance on Pv08 (Garzon and Blair 2014).

Table 1.6 Enumeration of mapping of simply-inherited CS traits and CS QTLs associated with resistance in common bean

Disease	Gene symbol	LG	Resistant parent	References
Angular Leaf spot (ALS)	*Phg-1*	1	AND277	Gonçalves-Vidigal et al. (2011)
	Phg-2, *Phg-2*^{2}	8	Mexico 54 BAT332	Namayanja et al. (2006), Mahuku et al. (2011),
	Phg-3	4	Ouro Negro	Gonçalves-Vidigal et al. (2013)
	Phg-4, Phg-5	4, 10	CAL143 G5686	Mahuku et al. (2009), Oblessuc et al. (2012), Keller et al. (2015)
Anthracnose (ANT)	*Co-1* *Co-1*^{2} *Co-1*^{3} *Co-1*^{4} *Co-1*^{5} *Co-1*^{HY} *Co-14* *Co-Pa* *Co-AC* *CoPv01*^{CDRK}	1	Michigan Dark Red Kidney Kaboon Perry Marrow AND277 Widusa Hongyundou Pitanga Paloma Amendoim Cavalo California Dark Red Kidney	McRostie (1919), Melotto and Kelly (2000), Melotto and Kelly (2000), Gonçalves-Vidigal et al. (2011), Gonçalves-Vidigal and Kelly (2006), Chen et al. (2017) Gonçalves-Vidigal et al. (2012) Lima Castro et al. (2017), Gilio et al. (2020) Gonçalves-Vidigal et al. (2020)
	Co-2	11	Cornell 49–242	Adam-Blondon et al. (1994)
	Co-3 *Co-15* *Co-16*	4	Mexico 222 Corinthiano Crioulo 159	Geffroy et al. (1999), Méndez-Vigo et al. (2005) Coimbra-Gonçalves et al. (2016)
	Co-4^3*/Co-3*^{3}	8, 4	PI207262	Alzate-Marin et al. (2007)

(continued)

Table 1.6 (continued)

Disease	Gene symbol	LG	Resistant parent	References
	Co-4 *Co-4²*	8	TO SEL1308	Fouilloux (1979) Young et al. (1998) de Arruda et al. (2000) Awale and Kelly (2001)
	Co-5 *Co-5²* *Co-6*	7	TU MSU 7–1 AB136	Young and Kelly (1996), Young et al. (1998), Sousa et al. (2014) Kelly and Young (1996), Gonçalves-Vidigal (1994)
	Co-4²/Co-5²/Co-3⁵	8, 7, 4	G2333	Young et al. (1998)
	Co-11	-	Michelite	Gonçalves-Vidigal et al. (2008)
	Co-12		Jalo Vermelho	Gonçalves-Vidigal et al. (2007)
	Co-13 *Co-17*	3	Jalo Listras Pretas SEL1308	Lacanallo and Gonçalves-Vidigal (2015) Trabanco et al. (2015)
Rust	*Ur-3, Ur-6, Ur-7, Ur-11, Ur-Dorado53, Ur-BAC6*	11	P94207 P94232 Beltsville DOR 364 BAC6 BelNeb-RR-1	Stavely (1998), Miklas et al. (2002)
	Ur-5, Ur-14, Ur-Dorado108	4	DOR 364 Ouro Negro Mexico309	Miklas et al. (2000), Souza et al. (2011)
	Ur-4	6	BAT93	Miklas et al. (2002)
	Ur-9,Ur-12	1, 7	PC50	Miklas et al. (2002)
	Ur-12	8	Kranskop	Mienie et al. (2005)
White mold (WM)	*WM1.1, WM1.2, WM2.4, WM7.1 WM8.2, WM8.3, WM9.1*	1, 2, 7, 8, 9	G122	Miklas et al. (2001)
	WM2.1, WM4.1, WM5.1, WM8.1	2, 4, 5, 8	PC-50	Park et al. (2001)

(continued)

Table 1.6 (continued)

Disease	Gene symbol	LG	Resistant parent	References
	WM2.2, WM2.3, WM5.2, WM7.2,WM8.4	2, 5, 7, 8	Bunsi	Kolkman and Kelly (2003), Ender and Kelly (2005)
	WM2.2, WM5.4, WM6.1, *WM7.5*	2, 5, 6, 7	I9365-31 VA19	Soule et al. (2011) Vasconcellos et al. (2017)
	WM3.3, WM7.5, WM9.2, WM11.1	3, 7, 9, 11	Tacana PI 318,695 PI 313,850	Mkwaila et al. (2011)
	WM1.3, WM3.1, WM6.2, WM7.1, WM7.4	1, 3, 6, 7	Xana	Vasconcellos et al. (2017)
Common Bacterial Blight (CBB)	*D2, D5, D7, D9*	2,5,7,9	BAT93	Nodari et al. (1993)
	CBB-2LL, CBB-2S, CBB-2P, CBB-2FL, CBB-1LL,	1, 2, 3, 4, 5, 6	BAC 6	Jung et al. (1996)
	Bng40, Bng139	7, 8	XR-235–1-1	Yu et al. (1998)
	FT-1, FT-2, LDT-2, Pod-1, Pod-2, Seed-1, Seed-2	1, 4, 5, 9	PX	Jung et al. (1997)
	CBLEAF, CBPOD	1, 2, 9, 10	BelNeb-RR-1	Ariyarathne et al. (1999)
	CBB-GH-leaf, CBB-GH-pod, CBB-GH-field	7, 10	DOR 364	Miklas et al. (2000)
	SU91, SAP6, Xa11.4^{OV1,OV3}	8, 10, 11	VAX1, VAX3	Viteri et al. (2015)
	Xa3.3^{SO}	3	BOAC 09–3	Xie et al. (2017)
Halo Blight (HB)	*HB83, HB16*	2, 3, 4, 5, 9, 10	BelNeb-RR-1	Ariyarathne et al. (1999)
	Rpsar-1, Rpsar-2	8,11	BAT93	Fourie et al. (2004)
	Pse-1, Pse-2, Pse-3, Pse-4, pse-5, Pse-6	2, 4, 10	UI-3 ZAA12 BelNeb-RR-1	Miklas et al. (2011, 20142009), Fourie et al. (2004)
	HB4.1, HB6.1	4, 6	Cornell 49–242	Trabanco et al. (2014)

(continued)

Table 1.6 (continued)

Disease	Gene symbol	LG	Resistant parent	References
	PDC^{3-}2, PDC^{4}-2, PDC^{5}-2, $SAUDPC^{3}$-2, $PLAUDPC^{3}$-2, $PAUDPC^{3}$-2, $PAUDPC^{4}$-2, SDC^{7}-6	2, 6	P1037 PHA1037	González et al. (2016)
	HB4.2, HB5.1	4, 5	PI 150,414 Rojo CAL 143	Tock et al. (2017)
BCMV/ BCMNV	*bc-1^{2},bc-u*	3	Olathe Sierra	Strausbaugh et al. (1999)
	bc-3	6	BAT93	Johnson et al. (1997)
	I	2	BelNeb-RR-1	Ariyarathne et al. (1999)
ClYVV	*cyv, desc*	3	Black Knight	Hart and Griffiths (2013)
WMV-2	*Hsw*, *Wmv*	2	Black Turtle-1 Great Northern 1140	Provvidenti (1974), Provvidenti (1987)
CpSMV	*Anv*, *Lnv*	2	Iguaçu Pitouco	Morales and Castano (1992)
BPMV	*R-BPMV*	2	BAT93	Thomas and Zaumeyer (1950), Pflieger et al. (2014)
CMV	*PvCMR1*	10	Othello	Seo et al. (2006), Meziadi et al. (2016)

Recently, co-segregation analysis inoculating $F_{2:3}$ families from the Rudá × Ouro Negro cross with of *C. lindemuthianum* (ANT) and *U. appendiculatus* (rust) races reported the genetic linkage between *Ur-14* and *Co-3*^{4} genes (Valentini et al. 2017). Hurtado-Gonzales et al. (2017) evaluated an F_2 population of Pinto 114 (susceptible) × Aurora (resistant *Ur-3*) for its reaction to four different races of *U. appendiculatus* and bulked segregant analysis using the SNP chip BARCBEAN6K_3 placed *Ur-3* on the lower arm of chromosome Pv11. Specific SSR and SNP markers and haplotype analysis of 18 sequenced bean varieties positioned *Ur-3* in a 46.5-kb genomic region from 46.96 to 47.01 Mb on Pv11. The authors identified in this region the SS68 KASP marker that is tightly linked to *Ur-3*, and validation of SS68 using a panel of 130 diverse common bean cultivars containing all known rust resistance genes showed SS68 to be highly accurate.

Genetic resistance to white mold (WM), caused by the fungus *Sclerotinia sclerotiorum*, is quantitatively inherited, and several QTLs have been identified thus far (Schwartz and Singh 2013). A comparative map composed of 27 QTLs for WM resistance and 36 QTLs for disease-avoidance traits was developed by Miklas et al. (2013). Recently, Vasconcellos et al. (2017) identified 37 QTLs condensed into 17 named loci (12 previously named and five new), nine of which were defined as meta-QTLs WM1.1, WM2.2, WM3.1, WM5.4, WM6.2, WM7.1, WM7.4, WM7.5, and WM8.3; these are robust consensus QTLs representing effects across different environments, genetic backgrounds, and related traits.

Bacterial Diseases

Common bacterial blight (CBB) caused by *Xanthomonas campestris* pv. *phaseoli* Smith (Dye) [synonymous with *X. axonopodis* pv. *phaseoli* (Smith) Vauterin et al.] recently reclassified by Constantin et al. (2016) as *X. phaseoli* pv. *phaseoli* is a severe disease of common bean worldwide (Singh and Schwartz 2010). CBB resistance is an inherited-quantitatively trait and, to date, 26 minor and major effect QTLs, that are responsible for resistance to CBB, have been reported across 11 linkage groups (Singh and Miklas 2015; Viteri et al. 2015). Among these, Viteri et al. (2015) identified the major QTL *Xa11.4*^{OV1,OV3} which explained up to 51% of the phenotypic variance for CBB resistance in leaves. Recently, a new isolate-specific QTL underlying CBB resistance was identified on Pv03 which showed an additive effect with SU91 QTL (Xie et al. 2017).

For halo blight (HB), caused by the bacterium *Pseudomonas syringae* pv. *phaseolicola* (Burkn.) Downs, qualitative and quantitative resistance genes have been reported (Ariyarathne et al. 1999; Fourie et al. 2004; Miklas et al. 2014; Trabanco et al. 2014; González et al. 2016; Tock et al. 2017). Five dominant (*Pse-1*, *Pse-2*, *Pse-3*, *Pse-4* and *Pse-6*) and one recessive (*pse-5*) genes were identified on chromosomes Pv02, Pv04, and Pv10 (Miklas et al. 2009, 2011, 2014). Two independent genes, *Rpsar-1* and *Rpsar-2* that confer AvrRpm1-specific resistance were located near genes that confer resistance to the *C. lindemuthianum* fungus (Fourie et al. 2004).

Furthermore, 76 main-effect QTLs that explained up to 41% of the phenotypic variation for HB resistance, and 101 epistatic QTLs were identified by González et al. (2016). Additionally, Trabanco et al. (2014) observed two minor-effect QTLs (*HB4.1* and *HB6.1*) that explained 11 and 12% of phenotypic variation. In the last years, Tock et al. (2017) reported a major QTL of race-specific resistance (*HB5.1*) from cv. Rojo and a major QTL of race-nonspecific resistance (*HB4.2*) from PI 150,414.

Viral Diseases

The dominant *I* gene is located at the end of chromosome Pv02 and imparts a broad resistance to at least 10 potyviruses infecting common bean, including Bean common mosaic virus (BCMV), Bean common mosaic necrosis virus (BCMNV), Clover yellow vein virus (ClYVV), Bean yellow mosaic virus (BYMV), Soybean mosaic virus (SMV), and Watermelon mosaic virus-2 (WMV-2), among others (McKern et al. 1992; Fisher and Kyle 1994; Berger et al. 1997; Hart and Griffiths 2015; Meziadi et al. 2017).

The *bc* recessive genes, which confer resistance to the Potyviruses BCMV and BCMNV in common bean, have been widely studied (Miklas et al. 2000; Meziadi et al. 2017; Feng et al. 2018). These genes either together or combined with the*I* locus, protect plants from common mosaic disease and from black root systemic necrosis (Meziadi et al. 2017). Recessive resistance is controlled by four genes that include three strain-specific genes *bc-1*, *bc-2*, and *bc*-3 and one strain-nonspecific gene *bc-u*, which seems to be required for the expression of the other *bc* genes (Drijfhout 1978; Strausbaugh et al. 1999). Moreover, there are two alleles for *bc-1* (*bc-1* and *bc-1*^{2}) and *bc-2* (*bc-2* and *bc- 2*^{2}). The *bc-u* and *bc-1* genes have been positioned at one end of Pv03, while *bc-2* has no defined genomic position (Miklas et al. 2000; Meziadi et al. 2016). Feng et al. (2018) reported that *bc-1* and *bc-2* recessive resistance genes affect systemic spread of BCMV in common bean. Moreover, the efficiency of the restriction of the systemic spread of the virus was greatly enhanced when the alleles of both genes were combined (Feng et al. 2018). On the other hand, the *bc-3* gene located on Pv06, has been identified as a gene belonging to the eIF4E gene family (Naderpour et al. 2010; Meziadi et al. 2016).Two recessive genes called *cyv* and *desc* located on Pv06 were reported to be allelic forms of *bc-3*, and confer resistance to other Potyvirus: ClYVV, encoding eIF4E factors (Hart and Griffiths 2013; Meziadi et al. 2016).

Two dominant *R* genes, named *Hsw* and *Wmv*, confer resistance against the Potyvirus WMV-2 and were mapped in the same region of the *I* locus. The *Hsw* gen was identified in genotype Black Turtle-1 while *Wmv* in Great Northern 1140 common bean genotype (Provvidenti 1974, 1987). These genes induce two distinct resistance phenotypes to WMV-2 viral strain (Meziadi et al. 2017).

R genes conferring resistance to virus have also being positioned at the*I* locus. This is the case of the *Anv* dominant resistance gene present in Iguaçu common bean genotype and *Lnv* in genotype Pitouco which confer resistance to the Bean rugose mosaic virus (CpSMV) (Morales and Castano 1992). Other *R* gene, called

R-BPMV, which is in the region of the*I*locus, confer resistance to Bean pod mottle virus (BPMV) and was described in BAT93 common bean genotype (Thomas and Zaumeyer 1950; Pflieger et al. 2014).

An *R* gene against Cucumber mosaic virus (CMV), called *PvCMR1* encodes a TNL protein and was located on chromosome Pv10 (Meziadi et al. 2016). *PvCMR1* was identified in Othello common bean cultivar (Seo et al. 2006). For resistance against Alfalfa mosaic virus (AMV), two monogenic genes, named *PvAmv* and *PvAmv-2* mediate local necrosis in Idaho common bean genotype and extreme resistance in Corbett Refugee genotype, respectively (Wade and Zaumeyer 1940; Provvidenti 1987). There are other resistance genes against viruses, with no defined genomic position, that have been described in common bean (reviewed by Meziadi et al. 2017).

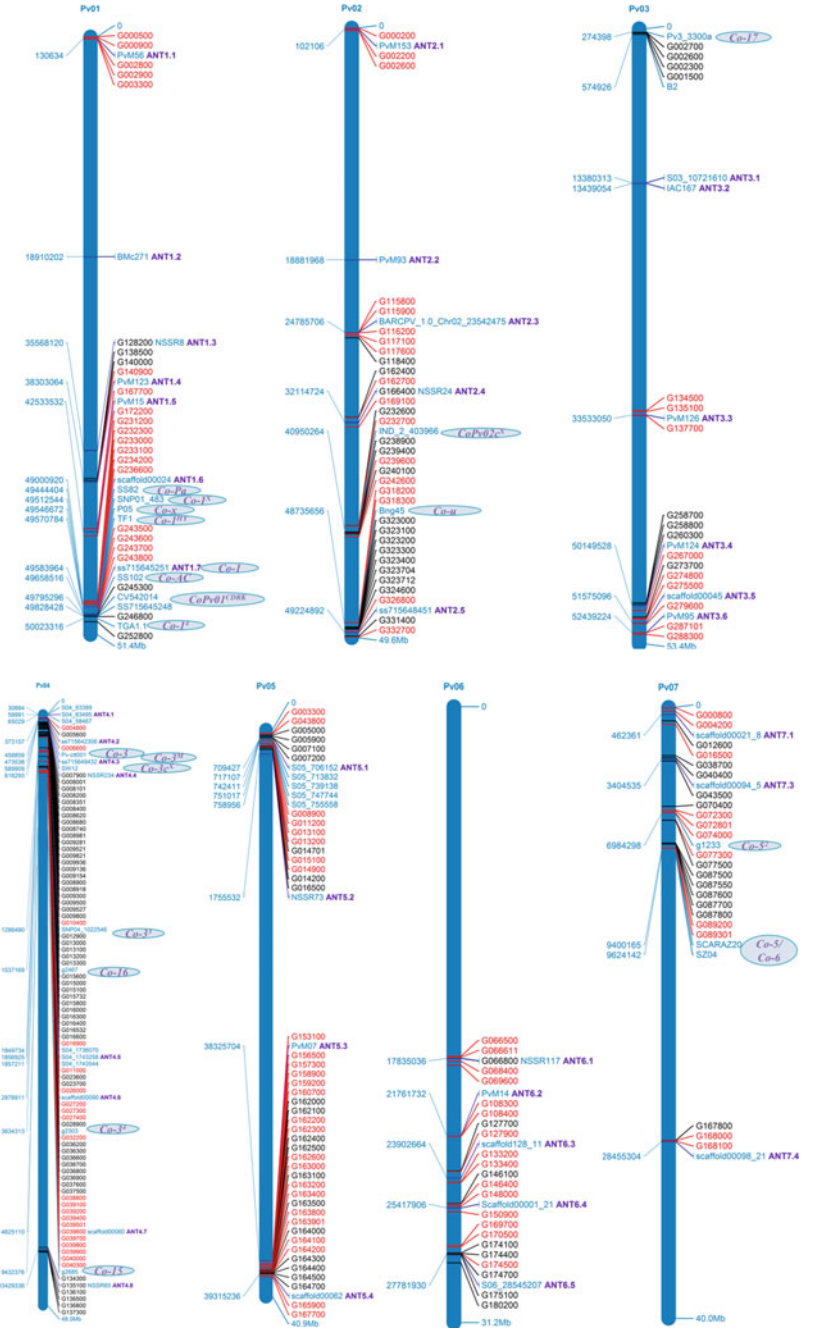
1.6.7 Framework Maps and Markers for Mapping CS QTLs

Previous studies have provided evidence for the existence of more than 20 ANT resistance genes that have been identified and mapped in common bean chromosomes Gonçalves-Vidigal et al. 2020). Furthermore, quantitative resistance loci (QRLs) have been described through genome-wide association studies (GWAS).

Identifying pathogen-responsive genes and proteins on a molecular level provides a better understanding of metabolic pathways involved in ANT resistance. Proteins with NBS-LRR domains are known to be encoded by most resistance genes. In addition, proteins with kinase domains are known to operate as pattern-recognition receptors that recognize pathogen-associated molecular patterns (PAMPs) and activate an immune response (Oblessuc et al. 2015; Meziadi et al. 2016; Vaz Bisneta and Gonçalves-Vidigal 2020).

Vaz Bisneta and Gonçalves-Vidigal (2020) reported a typical resistance protein located close to ANT resistanceloci in the common bean reference genome (Version 2.1). As typical resistance proteins, the authors investigated the ones with nucleotide-binding and leucine-rich repeat (NBS-LRR) domains and kinase domains. For this, first the authors collected available data in the literature about *C. lindemuthianum* resistance genes and Quantitative Resistance Loci (QRL). The physical position of ANT resistanceloci in the reference genome was identified performing a BLASTn search using the sequence of the molecular marker (linked to the ANT resistance gene) described in the literature. Additionally, model genes encoding proteins with NBS-LRR domains, kinase domains and tyrosine kinases that are located 500 kb upstream and downstream of the physical position of each ANT resistancelocuswere searched in phytozome.org.

Moreover, a chart with the selected candidate genes and ANT resistance loci located on the 11 chromosomes (Pv01 to Pv11) was built using the MapChart (Voorrips 2002). As a result, they obtained an integrated map containing candidate genes for all ANT resistance genes and Quantitative Resistance Loci previously described in the literature (Fig. 1.7). The integrated map contains a total of 256 NBS-LRR proteins and 200 protein kinase detected for anthracnose resistance. The authors


Pv01
Pv02
Pv03
Pv04
Pv05
Pv06
Pv07

◀**Fig. 1.7** An integrated map of common bean chromosomes with candidate genes encoding nucleotide-binding sites with leucine-rich repeats (NBS-LRR) and kinases proteins. Genetically characterized anthracnose resistance genes are displayed in circles. Genes that do not have a standardized name are represented by the symbol *Co* and an abbreviation of the cultivar name. Genome-wide association studies for anthracnose resistance loci are colored in purple, with the ANT symbol followed by the chromosome, it was mapped. Candidate genes are represented by the last seven digits from the annotation. For example, G000500 in Pv01 corresponds to *Phvul.001G000500*. Genes encoding NBS-LRR proteins and kinases are represented in black and red, respectively. Molecular markers are represented in blue (Vaz Bisneta and Gonçalves-Vidigal 2020)

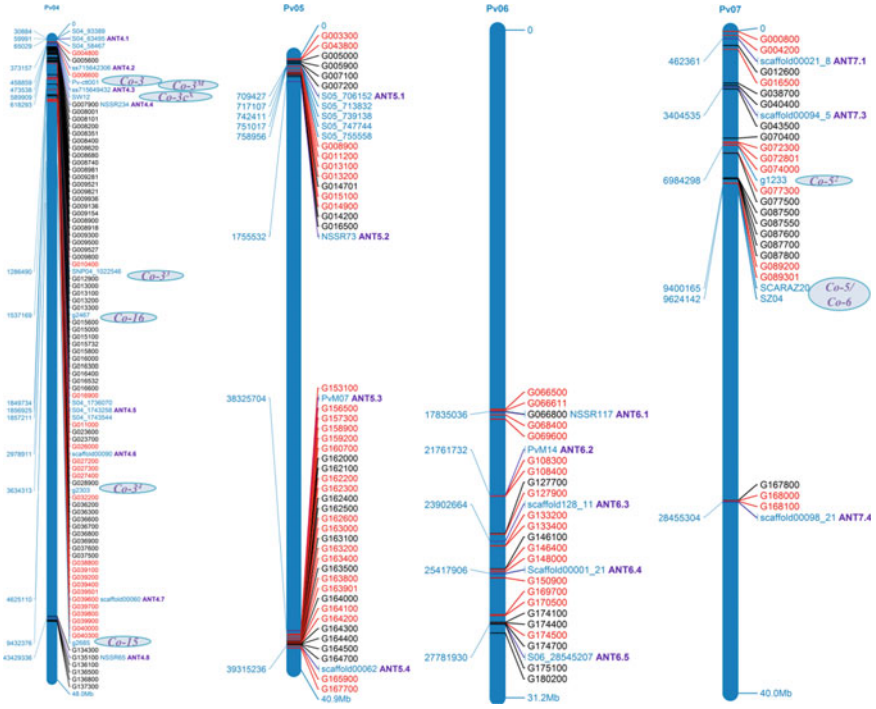


Fig. 1.7 (continued)

reported that the physical position and the molecular markers linked to these genes will be helpful to common bean breeders worldwide. Future validation of these candidate genes would be helpful to understand their function in anthracnose response and how they interact with metabolic pathways.

1.6.8 QTL Mapping Software Used

QTLNetwork is a software package for mapping and visualizing the genetic architecture underlying complex traits. It can simultaneously map QTLs with individual effects, epistasis, and QTL-environment interaction. Population data from F_2, backcross, RILs, and double-haploid populations, as well as populations from specific mating designs (immortalized F_2 and BC_nF_n populations) can be used. The Windows version of QTLNetwork was developed with a graphical user interface. Alternatively, the command-line versions have the facility to be run in other prevalent operating systems, such as Linux, Unix, and macOS (Yang et al. 2008).

Windows QTL Cartographer maps QTLs in cross populations from inbred lines. WinQTLCart includes a powerful graphic tool for presenting mapping results and can import and export data in a variety of formats. WinQTLCart implements different statistical methods as Single-marker analysis, Interval mapping, Composite interval mapping, Bayesian interval mapping, Multiple interval mapping, Multiple trait analysis, and Multiple trait MIM analysis (Wang et al. 2012).

QTL IciMapping is software capable of building high-density linkage maps and mapping QTLs in biparental populations. The following functionalities are integrated within this software package: BIN (binning of redundant markers); MAP (construction of linkage maps in biparental populations); CMP (consensus map construction from multiple linkage maps sharing common markers); SDL (mapping of segregation distortion loci); BIP (mapping of additive, dominant, and digenic epistasis genes); MET (QTL-by-environment interaction analysis); CSL (mapping of additive and digenic epistasis genes with chromosome segment substitution lines); and NAM (QTL mapping in NAM populations). Some examples of output files generated by MAP include a summary of the completed linkage maps, a Mendelian ratio test of individual markers, estimates of recombination frequencies, LOD scores, genetic distances, and the input files for using the BIP, SDL, and MET functionalities. In BIP functionality, more than 30 output files are generated, including results at all scanning positions, identified QTLs, permutation tests, and detection powers for up to six mapping methods. Three supplementary tools have also been developed to display completed genetic linkage maps, to estimate recombination frequency between two loci, and to perform analysis of variance for multi-environmental trials (Meng et al. 2015).

1.6.9 Details on Traitwise QTLs

The objective of QTL mapping is to determine the loci conditioning variation in complex quantitative traits. Because environments highly influence characteristics controlled by multilocus, it is necessary to evaluate the response of QTLs in different environments. Through QTL analysis it is possible to determine the number, the

location, the interaction of loci, as well as the actual genes and their responsive function.

Studying QTLs for important agronomic traits (e.g., yield) can lead to the development of improved crop varieties through plant breeding. Once a QTL is identified, regression analysis (R^2) can be performed to infer the proportion of phenotypic variance explained by the QTL. A large proportion of a quantitative variation explained by a significant QTL is designed for major QTLs. Usually, major QTLs exhibit R^2 from 10 to 30%, whereas significant QTLs with lower R^2 are called minor QTLs.

The LOD score compares the likelihood of a dataset exhibiting r crossovers out of a potential N between a pair of markers under the hypothesis of linkage (i.e., $\theta < 0.5$, where represents the recombination fraction) versus the same observation under the hypothesis of independent segregation (i.e., $\theta = 0.5$): $\text{LOD} = Z(\theta) = \log10((1\text{-}\theta)^{N-r} \times \theta r) /0.5^{N}$.

The LOD function is maximized at $\theta = r/N$, the maximum likelihood estimates of θ, and the convention that $Z(\theta) > 3$ lends strong support for linkage between the two markers is used frequently in mapping analysis. This value corresponds to a likelihood of observing the dataset, given that the two markers are unlinked, of < 1/1000. Given a prior probability of linkage for two markers chosen at random of 0.02, this likelihood corresponds to a probability $P < 0.05$ of a false positive (Cheema and Dicks 2009). The QTL confidence interval is located around the max LOD. The confidence region corresponds to a decline of 1 LOD from the peak.

The genetic regulation of quantitative traits is often complex due to their polygenic nature. However, QTL analysis is a useful approach for identifying chromosomal regions harboring genes that control quantitative traits. Besides mapping QTLs of the main effect, understanding epistatic interactions between QTLs is important. González et al. (2015) studied the genetic basis of quantitative resistance to two races of *C. lindemuthianum* of a segregating common bean RIL population from the cross PMB0225 × PHA1037.

Using a multi-environment QTL mapping approach, the authors identified race-specific anthracnose resistance QTLs showing significant main additive effects and observed epistatic interactions that explained phenotypic variation beyond those controlled by the main effects of individual loci. Another study (Yuste-Lisbona et al. 2014) identified single-locus and epistatic QTLs, as well as their environment interaction effects for six common bean pod traits (width, thickness, length, size index, beak length, and color). For this, Yuste-Lisbona et al. (2014) used an Andean intragene pool RIL population from a cross between a cultivated common bean and an exotic lima bean. Five QTLs with only individual additive effects and six with only epistatic effects were identified, and 12 QTLs showed both effects. Overall, the results obtained showed that additive and epistatic effects are the major genetic basis of pod size and color traits. The mapping of QTLs including epistatic loci provides support for implementing marker-assisted selection toward the genetic improvement of common bean.

Oblessuc et al. (2012) studied QTLs controlling resistance to angular leaf spot (ALS) using 346 RILs from the IAC-UNA × CAL 143 cross. The experiments were performed two years in the field and one year in the greenhouse, and data was analyzed

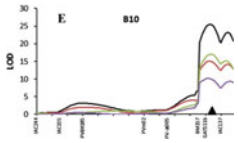


Fig. 1.8 QTL graph indicating the LOD score values for each marker position. LOD scores obtained via joint CIM analysis (y) using the molecular marker distances of the IAC-UNA × CAL 143 cross genetic map for each experiment (dry season, red; wet season, green; and greenhouse, purple) and joint analysis (black). Black triangles indicate the position of maximum LOD values for significant QTLs. Linkage group 10 is indicated as B10 (Oblessuc et al. 2012)

by joint composite interval mapping for QTL x environment interaction. As a result, the authors identified seven QTLs mapped on five linkage groups. Among these, *ALS10.1*^{DG,UC}, found linked to the GATS11b marker on linkage group B10, presented major effects (R^2 between 16 and 22%). This QTL could be important for bean breeding, as it was stable in all environments, and the GATS11b marker is a potential tool for marker-assisted selection for ALS resistance. A QTL graph indicating the LOD score values for each marker position for linkage group 10 is shown in Fig. 1.8. The QTL *ALS5.2* showed an important effect (9.4%) under inoculated conditions in the greenhouse. *ALS4.2* was another major QTL, under natural infection in the field, explaining 10.8% of the variability for resistance reaction. The other QTLs showed minor effects on resistance.

Elias (2018) studied 160 RILs derived from the cross between IAPAR 81 × LP97-28 held under conditions of drought stress and non-drought stress for two years, for QTL mapping. For this, 773 SNP markers were used to construct linkage groups covering 815.9 cM of the bean genome, with distance of 1.34 cM between markers. As a result, the authors identified 16 QTLs on chromosomes Pv01, Pv02, Pv03, Pv05, Pv07, Pv08, Pv09, Pv10, and Pv11 (Fig. 1.9).

1.7 Association Mapping Studies

1.7.1 Extent of Linkage Disequilibrium

Linkage disequilibrium (LD) is the non-random association of alleles at two loci (Mackay and Powell 2007) and constitutes the base of gene identification by association mapping. Association mapping is based on the detection of quantitative trait loci (QTLs) by evaluating the patterns of genome-wide LD in a diverse panel and studying the association between relevant phenotypes and genomic variants. An example of linkage disequilibrium observed in common bean chromosome Pv04 using 115 accessions genotyped with 5,398 SNP markers on the BARCBean6K_3 Illumina BeadChip can be observed in Fig. 1.10.

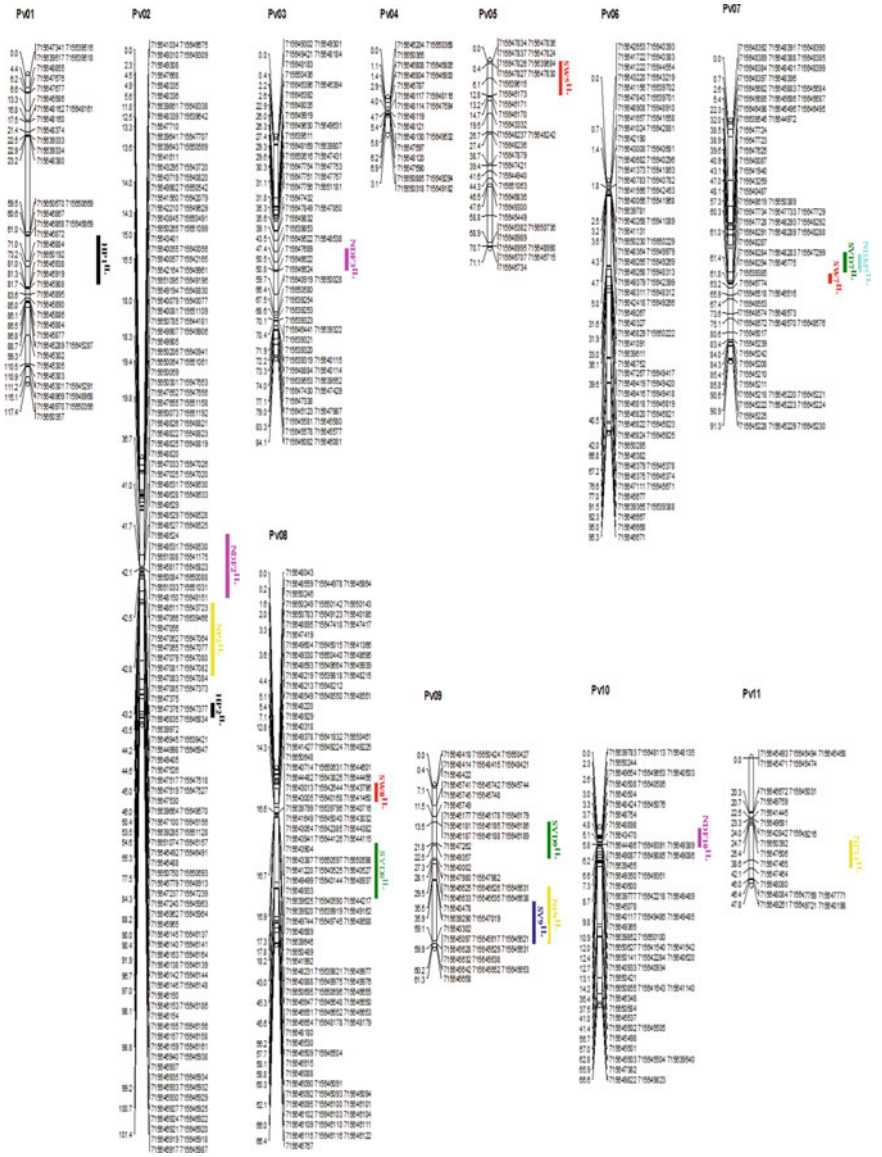


Fig. 1.9 Genetic mapping for the RIL population Iapar81 × LP97-28 cross using 773 SNPs markers assigned to the 11 common bean linkage groups. QTL locations were mapped using the Composite Interval Method (CIM) of the Win cartographer software and the LOD thresholds calculated based on 1000 permutations. A total of 16 QTLs were associated with the yield per day, the weight of 100 grains, number of pods per plant, the height of the plant, number of days for flowering, and number of days for maturation under water stress conditions (Elias 2018)

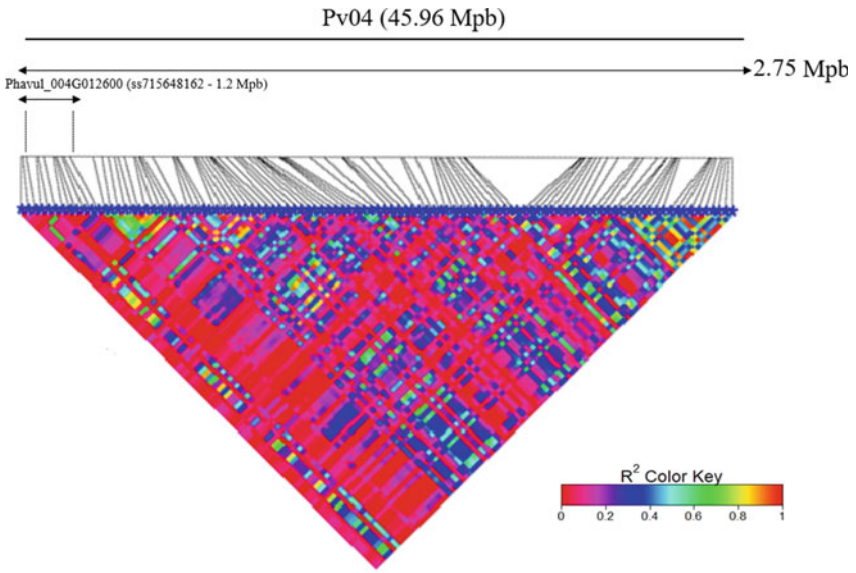


Fig. 1.10 Linkage disequilibrium observed in common bean chromosome Pv04 using 115 accessions genotyped with 5,398 SNP markers on the BARCBean6K_3 Illumina BeadChip (Vidigal Filho et al. 2020)

With the development of a reference genome for the common bean (Schmutz et al. 2014; Vlasova et al. 2016), and the availability of high-throughput genotyping platforms (Hyten et al. 2010; Goretti et al. 2014; Gujaria-Verma et al. 2016), genome-wide association study (GWAS) mapping has become a powerful and efficient tool for discovering novel genes of complex agronomic traits. However, in association mapping, population structure and kinship among individuals must be considered to avoid the emergence of false associations. If not considered as part of the analysis, structure in the population used in association mapping can lead to spurious associations, since in a structured population the LD increases if the allele frequencies between loci vary between the subpopulations that comprise it (Oraguzie et al. 2007). Vidigal Filho et al. (2020) reported that the ss71568162 marker, positioned at 1,224,240 bp, encompasses the Phvul.004G012600 candidate gene, which encodes a serine-threonine protein kinase conferring resistance to race 73 of *C. lindemuthianum* (Fig. 1.8).

1.7.2 Target Gene-Based LD Studies

Association mapping is a powerful tool that allows the identification of loci whose contribution explains part of the observed phenotypic variation. The advantage of association mapping over conventional biparental QTL mapping lies in improving

the resolution of association studies between markers and phenotypes, achieved by using a larger population that involves a greater number of alleles. Mapping based on biparental populations relies on creating experimental populations derived from controlled crossing and allows only a limited amount of genetic variation to be analyzed. Alternatively, association mapping, based on population-scale samples, allows the analysis of a wider range of natural variation (Burghardt et al. 2017). Furthermore, the smaller number of recombination events during biparental population generation makes it harder to locate a QTL with high resolution, whereas association mapping, by taking advantage of recombination events over multiple generations in a lineage, allows a finer resolution for the location of QTLs (Han and Huang 2013; Burghardt et al. 2017). Thus, association mapping further improves genetic resolution, includes a greater number of alleles and traits, and reduces research time (Korte and Farlow 2013; Xu et al. 2017).

Association mapping approaches can be classified into two types: (1) candidate gene (CG) association mapping and (2) genome-wide association study (GWAS) mapping. The first is based on selecting genes potentially involved in controlling the phenotypic variation of the trait under study. This approach aims to identify mutations and causal genes in a small number of CGs within a specific genomic region and requires a good knowledge of the genetics and biochemistry of the trait. The second approach, GWAS mapping, is a broad genome-wide study attempting to identify variation associated with phenotypic diversity and requires large, highly diverse association panels and a great number of well-distributed molecular markers (González et al. 2017). Considering that GWAS requires extensive genotypic and phenotypic information, it is more usefully applied in major crops, which may already have available resources and in which a wide research community may be interested in developing future resources (Mousavi-Derazmahalleh et al. 2019). Thus, factoring in its great genetic diversity, the common bean is a good target for GWAS (Blair et al. 2009).

1.7.3 Genome-Wide LD Studies

GWAS mapping has become an emerging approach to discover QTLs associated with agronomic and phenological traits (Galeano et al. 2012; Kamfwa et al. 2015a), symbiotic nitrogen fixation (Kamfwa et al. 2015b), drought tolerance (Hoyos-Villegas et al. 2017), and disease resistance (Shi et al. 2011;Hart and Griffiths 2015;Perseguini et al. 2016;Zuiderveen et al. 2016;Tock et al. 2017; Oladzad et al. 2019a). Shi et al. (2011) were the first to apply GWAS to identify disease resistance loci in common bean. A population of 395 dry bean lines of different market classes were evaluated for CBB resistance and genotyped using 132 SNPs evenly distributed across the genome. Twelve significant SNP markers co-localized with or close to previously identified CBB-QTLs. Moreover, eight new resistance loci were identified. Hart and Griffiths (2015) conducted a case–control GWAS approach to identify SNPs associated with resistance to bean yellow mosaic virus (BYMV), which is conditioned by the *By-2*

allele. They genotyped a set of recombinant inbred lines (RILs), derived from an introgression program, with 7,530 SNPs and identified 44 GBS SNPs associated with the resistance phenotype, which mapped onto the distal portion of chromosome Pv02. Seven of these SNPs were converted to KASP assays and shown to be tightly linked to BYMV resistance in an F_2 population of 185 individuals (Hart and Griffiths 2015).

Quantitative resistance loci (QRL) controlling resistance to both ANT and ALS diseases of 180 common bean accessions were identified by Perseguini et al. (2016) using GWAS. A total of 17 SSR and 21 SNPs associated with resistance to ANT Race 4 were detected. Moreover, 11 SSR and 17 SNPs associated with resistance to Race 0–39 of *Pseudocercospora griseola* were detected. The greatest number of loci associated with ANT resistance were in chromosomes Pv03 and Pv08, while chromosome Pv04 was the most saturated one, with six markers associated with ALS resistance. The authors reported three markers that were associated with both diseases, SSR-IAC167 and PvM95, both located on chromosome Pv03, and the SNP scaffold00021_89379 located on chromosome Pv07. Fritsche-Neto et al. (2019) performed a GWAS using 60 inbred elite lines, developed by the Embrapa (The Brazilian Agricultural Research Corporation) common bean breeding program across 22 years, to identify markers linked to ANT and ALS resistance. The lines were evaluated under field conditions and genotyped with 5,398 SNPs. Two SNPs associated with ANT resistance loci on chromosome Pv02 and one SNP associated with ALS resistance loci were observed. Recently, Vidigal Filho et al. (2020) conducted a GWAS approach using 115 accessions from five Brazilian states, revealing new sources of ANT and ALS resistance. The authors reported SNP markers associated with resistance to ANT races 9 and 73 that were positioned on chromosome Pv04; resistance to race 65 on chromosomes Pv01, Pv04, and Pv08; and resistance to races 2047 and 3481 on chromosomes Pv10 and Pv05, respectively. Furthermore, SNPs associated with resistance to race 63–39 of *P. griseola*, were mapped on chromosomes Pv03, Pv06, and Pv08, whereas for race 31–23, SNPs were mapped on chromosomes Pv02 and Pv04.

Nine disease resistance loci for ANT and seven for CBB have been detected by Wu et al. (2017) using NBS-SSR markers and GWAS. Three of these loci (NSSR24, NSSR73, and NSSR265) were located at new regions for ANT resistance, while the other two (NSSR65 and NSSR260) were located at new regions for CBB resistance. Furthermore, the SSR marker NSSR65, located on chromosome Pv04, was associated with both diseases, suggesting a possible pleiotropic effect.

Diversity panels that capture variation among a defined population are essential for discovering the genome-wide effects that control specific phenotypes (McClean and Raatz 2017). Recently, common bean geneticists and breeders developed the Andean Diversity Panel (ADP) (Cichy et al. 2015) and the Mesoamerican Diversity Panel (MDP) (Moghadam et al. 2016), which were assembled to represent the genetic diversity of cultivated beans within each major gene pool and to facilitate gene pool-specific genetic analyses. Each panel consists of modern genotypes commonly used by growers in production fields, and they are useful for GWAS mapping since they have been SNP genotyped with approximately 200,000 SNPs (McClean and

Raatz 2017). After genomic characterization, because of the homozygous nature of common bean varieties, the genetic data can be used many times to evaluate different phenotypes across different environments (González et al. 2017). The ADP consists of 504 Andean accessions, whose descriptions are available on the USDA-ARS Feed the Future-Bean Research Team website (http://arsftfbean.uprm.edu/bean/?p=472). The ADP has been used in recent GWAS mapping to identify disease resistance loci, including resistance to halo blight (Tock et al. 2017), anthracnose (Zuiderveen et al. 2016), and to root pathogens like Fusarium solani (Vasquez-Guzman, 2016; Zitnick-Anderson et al. 2020), *Pythium* spp. (Soltani et al. 2018; Dramadri et al. 2020), and *Rhizoctonia solani* (Oladzad et al. 2019b).

Despite the potential that association mapping presents for identifying complex genes, its limitations include the tendency for spurious association, identification of small-effect variants, missing genotypes, and genetic heterogeneity (Korte and Farlow 2013). Further, association mapping resolution depends on the rate of LD decay, so a better foundation could be using wild relatives of crops (Mousavi-Derazmahalleh et al. 2019). In this way, a total of 317 plant introductions (landraces and wild bean accessions) from the USDA core collection was used to conduct a GWAS to identify markers linked to the soybean cyst nematode (SCN, *Heterodera glycines*) resistance loci (Jain et al. 2019). Analyses were conducted separately for the Andean and Mesoamerican groups, using 3,985 and 4,811 SNP markers, respectively. Significant SNPs on Pv07 and Pv11 in the Mesoamerican group, and Pv07, Pv08, Pv09, and Pv11 in the Andean group, were found to be associated with SCN resistance. Moreover, homologs of soybean *rhg1*, a locus which confers resistance to SCN in soybean, were identified on chromosome Pv01 in the Mesoamerican group and on Pv08 in the Andean group.

Another study of genotyping-by-sequencing analysis and 19 climatic characteristics obtained through the WorlClim site was carried out by Elias (2018), in which a set of 110 common bean accessions previously genotyped using a sequencing genotyping methodology was evaluated, producing 28,823 SNPs. Through associative mapping, it was possible to detect loci of quantitative characteristics, for a total of 135 associations between characteristics vs. markers (Bonferroni test <0.5%). Of the 19 bioclimatic traits, eight exhibited significant associations, and associations for seasonality of temperature and precipitation in the driest quarter were found on Pv09, with $R^2 = 36.26\%$ and 36.46%, respectively. Associations between markers and climatic variables were distributed throughout common bean LGs, except for Pv08. The results show a correlation between markers and climatic characteristics on a national scale, helping to identify candidate genes for regional adaptation. These considerations are of great relevance for the conservation and exploration of genetic diversity between and within common bean accessions in Brazil (Elias 2018).

The SNP markers and candidate genes found associated with the resistance should be validated in segregating populations, which could further be used for marker-assisted selection. As a result, breeding programs might be able to develop resistant common bean cultivars to several diseases.

1.8 Marker-Assisted Breeding for Resistance/Tolerance Traits

1.8.1 Germplasm Characterization and Distinctiveness, Uniformity, and Stability (DUS)

Germplasm characterization is the recording of distinctly identifiable and highly heritable characteristics. Germplasm evaluation refers to the agronomic description of GenBank material, including traits that are generally important to breeders and researchers in crop improvement.

Germplasm characterization enables quick and easy discrimination among phenotypes and is essential to provide information on accessions' traits, assuring the maximum utilization of the germplasm collection for the final users. Evaluating genetic diversity and population structure is necessary to improve a population through plant breeding because it informs decisions such as parental selection and long-term conservation of important germplasm (Acosta-Gallegos et al. 2007; Bitocchi et al. 2012; Piñón et al. 2020).

Molecular markers are replacing morphological descriptors for some purposes, such as evolutionary studies, assessment of interrelationships among accessions and geographic groups of accessions, estimating genetic diversity, and identifying duplicates. However, the evaluation of visible descriptors will remain important for identifying landrace accessions at the field level as an adjunct using molecular markers. A descriptor can be a numeric value such as weight, length, or output from a sensor; a code within a scale, such as a 1 to 9 rating for disease severity, or a rating for shade and color intensity; or a qualifier, such as a trait's absence or presence. The main aims of germplasm characterization are to: describe accessions and establish their diagnostic characteristics; classify accessions into groups using sound means; assess interrelationships among accessions or traits, and among geographic accession groups; estimate the extent of variation in a GenBank collection; and identify duplicates in a collection.

In accordance with the UPOV (2015), varieties can be considered distinct where they have a different expression in a grouping character, such as growth type in plants and pigmentation of the hilum in seeds. Distinctness must be statistically evaluated, with a significant difference at 1% ($P = 0.01$) significance level in at least one character, in a combined over years distinctness analysis of variance. Where the number of tested varieties is too small (below 15), giving insufficient degrees of freedom for the COYD analysis to be valid, then a standard of significant differences using the one-year "t" criterion at 5% is used. Where varieties are grown nearby, under the same conditions, and direct comparisons can be made, distinctness can be determined via visual observation. In these circumstances, the basis for distinctness will be recorded with clarity. If the visual observation shows the two varieties are clearly distinct, then a case will be presented to APHA and the NLSC with any supporting evidence.

Uniformity is assessed for all characteristics used to establish distinctness and is based on the assessment of off-types (variants). Off-type plants in field-sown plots are identified by visual assessment and marked for a decision on recording omission depending upon incidence across replicates. Care is taken to ensure that the plants that are counted are not the result of any non-genetic factors, such as environment, pest, and disease. The assessment of off-types is undertaken in both test cycles, and the total combined should not exceed the following: population standard = 2%; acceptance probability = 95%. (For example: 6 off-types in a population of 160.) After all variants have been excluded, characteristics listed in distinctivenessare used to assess the uniformity of the remaining plants. Uniformity is based on the assessment of general variation where measurements are recorded. Provided a variety meets the off-type standard, it can be considered sufficiently uniform after two test cycles, if, for all measured characters necessary for distinctness, the Combined Over Years Uniformity (COYU) analysis is not significantly greater than that of the reference varieties at the 0.2% (P = 0.02) significance level.

A variety is considered sufficiently stable when there is no evidence to indicate that it lacks uniformity or fails to conform to the essential characteristics of its description in different submissions or in different tests.

The following 23 characteristics are recorded in distinctiveness,

Uniformity, and stability tests:

Foliage: intensity of green color (1 = light; 2 = light to medium; 3 = medium; 4 = medium to dark; 5 = dark).

Foliage: **greyish hue of green color** (1 = absent; 9 = present).

Time of flowering: (50% of plants with at least one open flower) (1 = very early; 3 = early; 5 = medium; 7 = late; 9 = very late).

Wing: melanin spot (1 = absent; 9 = present).

Wing: colour of melanin spot (1 = yellow; 2 = brown; 3 = black).

Standard: extent of anthocyanin coloration (Only varieties with Wing: melanin spot: present) (1 = small; 3 = medium; 5 = large).

Standard: intensity of anthocyanin coloration (Only varieties with Wing: melanin spot: present) (1 = weak; 2 = medium; 3 = strong).

Flower: length (1 = very short; 3 = short; 5 = medium; 7 = long; 9 = very long).

Standard: width (1 = narrow; 2 = narrow to medium; 3 = medium; 4 = medium to broad; 5 = broad).

Flower: ratio flower length/standard width (1 = low; 3 = medium; 5 = high).

Leaflet: length (basal pair of leaflets at second flowering node) (1 = very short; 3 = short; 5 = medium; 7 = strong; 9 = very strong).

Leaflet: width (1 = very narrow; 3 = narrow; 5 = medium; 7 = broad; 9 = very broad).

Stem: anthocyanin coloration (Only varieties with melanin spot) (1 = absent or weak; 3 = medium; 5 = strong).

Plant: growth type (1 = determinate; 2 = indeterminate).

Plant: length (1 = very short; 3 = short; 5 = medium; 7 = tall; 9 = very long).

Stem: number of nodes (up to and including first flowering node) (1 = very few; 3 = few; 5 = medium; 7 = many; 9 = very many).

Pod: length (without beak) (1 = very short; 3 = short; 5 = medium; 7 = long; 9 = very long).

Pod: width (from suture to suture) (1 = very narrow; 3 = narrow; 5 = medium; 7 = broad; 9 = very broad).

Pod: intensity of green color (1 = light; 2 = medium; 3 = dark).

Seed: shape (1 = circular; 2 = non-circular).

Seed: color of testa (immediately after harvest) (1 = light yellow brown; 2 = grey; 3 = green; 4 = black).

Seed: black pigmentation of hilum (1 = absent; 2 = present).

100 seed weight (1 = very low; 3 = low; 5 = medium; 7 = high; 9 = very high).

1.8.2 Marker-Assisted Gene Introgression

Molecular mapping and tagging of important genes have contributed to significant advances in marker-assisted selection (MAS) of crop breeding. Since molecular markers are related to nucleotide sequence variations, many tags have been developed for different types of plant crops. They also have several advantages over the traditional phenotypic markers (Mohan et al. 1997; Kole and Gupta 2004). In general, this method is faster, cheaper, and more accurate than traditional phenotypic assays. Consequently, it may provide higher effectiveness and efficiency in terms of time, resources and efforts. Besides that, MAS is not affected by the environment, which allows the selection to be conducted under any environmental conditions. In traditional phenotypic selection, an individual gene or loci might be masked by the effect of others. In contrast, MAS can simultaneously identify and select single Genes/QTLs in the same individuals, when traits are controlled by multiple Genes/QTLs. For that reason, it is particularly feasible for gene pyramiding.

The usage of MAS enables introgression of resistance genes into a cultivar, decrease of population size, and time required to develop a new variety. Methods to characterize disease resistance genes have changed over time. Initial work with RFLP, AFLP and, RAPD markers were followed by a series of SSR, SCAR, and SNP marker systems, providing suitable markers for breeding purposes. These markers linked to single-gene traits have been successfully used in MAS (Singh and Schwartz 2010). Thus, gene introgression using MAS allowed the development of numerous common bean lines with resistance to angular leaf spot (Oliveira et al. 2005), anthracnose (Alzate-Marin et al. 1999; Miklas et al. 2003), rust (Stavely 2000), common bacterial blight (Miklas et al. 2006b) and bean gold yellow mosaic virus (Miklas et al. 2002). In addition, two major white mold resistance QTLs have been successfully introgressed using MAS with a positive asset in the target traits (Ender et al. 2008). The use of MAS in breeding for resistance to biotic and abiotic stress in common bean has been widely reviewed by Miklas et al. (2006a). The latest publication about the common bean reference genome (Schmutz et al. 2014) allowed mapping and

comparison of several SSR, SCAR, and SNP markers' positions. Some of them were mapped in different chromosomes than the ones originally reported. In the last few years, GBS, GWAS, and WGS techniques improved plant breeding by making it quickly and efficiently through the usage of MAS.

1.8.2.1 Gene Tagging and Marker-Assisted Selection for Bean Diseases

Conventional breeding methods used depend on visual screening of genotypes to select for traits of economic importance. Nevertheless, success using this method depends on its reproducibility and heritability of the characteristic. MAS is an excellent methodology for common bean breeders who also work to improve disease resistance. On behalf of MAS to be highly effective, a high association and tight linkage must exist between the genes for resistance to diseases and molecular markers and easy to evaluate (Yu et al. 2004). As mentioned in the previous section, associations between resistance genes and molecular markers are widely used for mapping genes to specific linkage groups. Since the last century, several studies have used molecular markers to select qualitative resistance to anthracnose (ANT), angular leaf spot (ALS), common bean mosaic virus (BCMV), and rust diseases.

Anthracnose

Garzón et al. (2007) were the first to evaluate the efficiency of marker-assisted selection (MAS) to detect anthracnose resistance. For that purpose, a series of backcross plants, using PCR-based markers SAB3 and SAS13 linked to *Co-5* and *Co-4*^{2} genes, were used. The authors concluded that *Co-5* is associated with SAB3, whereas *Co-4*^{2} is linked to SAS13. Likewise, Vidigal Filho et al. (2008) evaluated backcross F_2BC_3 lines using a $SAS13_{950}$ marker and observed that it was linked to a *Co-4*^{2} allele. Two hundred and thirty-three BC_3F_2 near-isogenic lines containing a *Co-4*^{2} resistance allele in various combinations were developed through MAS for the resistance genes and phenotypic selection for anthracnose. The BC_3F_2 NILs having a *Co-4*^{2} resistance allele showed a wider resistance spectrum and manifested increased levels of resistance to race 2047 of *C. lindemuthianum*. Out of the 233 BC_3F_2 lines analyzed by molecular markers, 80 of them revealed the presence of $SAS13_{950}$ linked to a *Co-4*^{2} allele. Moreover, Brazilian cultivars Awauna UEM and Flor Diniz UEM, both resistant to anthracnose, were obtained by five backcrossings with a $SAS13_{950}$ marker through MAS (Gonçalves-Vidigal, personal communication). Different anthracnose and common bean mosaic genes were pyramided by Ferreira et al. (2012) using the pedigree method from a single cross between lines obtained in the introgression step: lines A1699 (derived from cross A1258 × A1220), A2438 (A1220 × A1183), A2806 (A1878 × 2418), and A3308 (A1699 × A2806). Additionally, seven molecular markers known to be linked to resistance loci were used, and it was possible to differentiate 11 fabada lines. As a result, the authors reported a new fabada line A3308

containing resistance to three anthracnose races controlled by genes included in clusters *Co-2* and *Co-3/9*, and to common bean mosaic genes with genetic resistance controlled by genotype *I* + *bc-3*.

Rust

On the subject of rust, the first resistance gene tagged in common bean was *Ur-4* gene (Miklas et al. 1993), using the molecular marker $OA14_{1100}$. This marker was used to perform assisted selection of plants containing *Ur-4* (Kelly et al. 1993). However, its usage is restricted to Mesoamerican cultivars, since progenies from a cross between Early Gallatin and Andean cultivar do not segregate for $OA14_{1100}$ marker (Miklas et al. 1993). Previous studies reported limitations of molecular markers linked to *Ur-3* gene (Haley et al. 1994; Nemchinova and Stavely 1998; Stavely 2000). However, Valentini et al. (2017) developed several SSR markers linked to *Ur-3, Ur-4, Ur-5, Ur-11, Ur-14,* and *Ur-PI310762* genes. For that, accurate phenotyping for the inheritance of resistance studies, bulk segregant analysis (BSA) combined with high-throughput genotyping using the SNP chip BARCBEAN6K_3, were used. Following the same line of experiments, further SSR and SNP markers closely linked to *Ur-3* were developed based on BSA, SNP assay, and whole-genome sequencing methodologies (Hurtado-Gonzales et al. 2017). Interestingly, KASP SNP marker SS68 reliably distinguished cultivars containing *Ur-3* alone or in combination with other genes (Hurtado-Gonzales et al. 2017). Recently, co-segregation analysis inoculating $F_{2:3}$ families from the Rudá × Ouro Negro cross with of *C. lindemuthianum* (ANT) and *U. appendiculatus* (Rust) races reported the genetic linkage between *Ur-14* and $Co\text{-}3^4$ genes (Valentini et al. 2017).

White Mold

QTLs for white mold on linkage groups Pv02 and Pv07 from an ICA Bunsi × Newport Middle American dry bean population were identified by Kolkman and Kelly (2003). In ICA Bunsi × Raven Middle American dry bean populations, QTLs were also detected and mapped on linkage groups Pv02, Pv05, Pv07, and Pv08 (Ender and Kelly 2005). Later, Miklas et al. (2007) found two QTLs in a Pinto 3 navy beans (Aztec/ND88–106–04), which were mapped on linkage groups Pv02 and Pv03. Interestingly, the QTL described on Pv02 was identified previously in populations of ICA Bunsi 3 navy and ICA Bunsi 3 black bean RIL.

Further, a comparative study revealed the presence of QTLs in two separate populations, 'Benton'/VA19 (BV) and 'Raven'/I9365-31 (R31) crosses (Soule et al. 2011). For the first one, WM2.2 and WM8.3 were described for the greenhouse straw test and field resistance. In contrast, WM 2.2, WM4.2, WM5.3, WM5.4, WM6.1, WM7.3 were found in the Raven/I9365 -31 (R31) for greenhouse straw test and field resistance.

In addition, two QTLs were characterized in 'Tacana' × PI 318,695 (linkage groups Pv04 and Pv07) and Tacana × PI 313,850 (linkage groups Pv02 and Pv09) inbred backcross lines, using the greenhouse straw test (Mkwaila et al. 2011). Recently, an evaluation of the RIL population from the AN-37 × P02630 cross demonstrated the presence of 13 QTLs for agronomic and disease-related traits (Hoyos-Villegas et al. 2015).

Fusarium Root Rot

Resistance to FRR is quantitatively inherited and is strongly affected by environmental factors. QTLs associated with this disease varied between studies and populations. Due to limited genomic coverage of the available markers, a comparison of the physical positions of those QTLs was not suitable (Schneider et al. 2001; Chowdhury et al. 2002). In 2005, Román-Avilés and Kelly identified nine QTLs in crosses 'Negro San Luis' × 'Red Hawk' and 'Negro San Luis' × C97407. Later, five regions on linkage groups Pv03, Pv06, and Pv07 associated with QTL for FRR in an Eagle/Puebla 152 population were identified (Navarro et al. 2004). Most recently, two QTLs associated with FRR for greenhouse straw test and field resistance were mapped on Pv02 (Wang et al. 2018).

Common Bacterial Blight

In the early 2000s, important historical research steps towards MAS were taken. PI 319,443 resistance was introgressed into the common bean breeding line XAN 159. By doing that, two major QTLs for common bacterial blight resistance were defined: SCAR marker SU91 (Pedraza et al. 1997) found in Pv08, and BC420 marker detected in linkage group Pv06 (Yu et al. 2000a). Yu et al. (2000b) evaluated cosegregation of two polymorphic markers and only the $BC420_{900}$ revealed a significant association with a major QTL, which conferred resistance in HR67 to CBB. Following that, another major resistance QTL in OAC Rex was mapped on Pv05 (Bai et al. 1997; Tar'an et al. 2001; Michaels et al. 2006). Recently was reported the full genome sequence of the common bean OAC-Rex with introgression from the tepary bean, *P. acutifolius* (Perry et al. 2013). However, a negative association of seed yield with the SU9 marker linked with CBB resistance QTL derived from tepary bean was reported (O'Boyle et al. 2007). Furthermore, Miklas et al. (2009) addressed the presence of SH11.800, SR13.1150, and ST8.1350 markers linked to *Pse-1* and mapped on Pv10.

Bean Common Mosaic Virus

Since BCMV resistance genes are independent in the common bean, it contributes to the use of gene pyramiding as an approach for durable resistance (Zuiderveen et al. 2016). In 1994, Raven was released as the first common bean cultivar resistant

to BCMV (Kelly et al. 1994). The aforementioned cultivar carries two genes: one dominant hypersensitive *I* and one recessive *bc-3,* both confirmed by RAPD markers. This combination has been recognized for its durability over single gene resistance to both BCMV and BCMNV (Kelly 1997). SCAR markers based on OC11350/420 (ROC11) and OC20460 RAPD markers linked to *bc-3* gene were also developed (Johnson et al. 1997). However, the use of these markers in MAS have been limited in common bean because of a lack of polymorphism and reproducibility across different genetic backgrounds and gene pools (Kelly et al. 2003).

Pedigree selection through the F_7 generation based on superior agronomic features (early maturity, erect plant architecture, and good pod set) and commercial seed type, Bella cultivar was created. Derived from cross 'Verano'//PR0003-124/ 'Raven', Bella combines resistance to BCMV, BCMNV, BGYMV and web blight (Beaver et al. 2018).

1.8.3 Gene Pyramiding

Conventional breeding methods involve the complex selection of several genotypes harboring different resistance genes, which can affect the accuracy and efficiency of the process. However, gene pyramiding, developed from a single cross between lines obtained during introgression, using either a pedigree or backcross method, is a good strategy for durable resistance and can facilitate a MAS approach (Ashikari and Matsuoka 2006). Gene pyramiding combines multiple desirable genes from multiple parents into a single genotype for a specific trait. Thus, this method enhances genetic resistance of bean cultivars.

Marker-assisted gene pyramiding: pyramiding aims to assemble multiple genes or QTLs into a single genotype (Ashikari and Matsuoka 2006). Pyramiding and the introgression of multiple genes/QTLs affecting the same phenotypic trait remains a daunting challenge due to complexity in phenotypic selection methods, and more often, is exacerbated by epistatic interactions. However, large-scale genotyping facilities revolutionized MAS in the breeding system by considerably reducing the span of breeding cycles and facilitating gene pyramiding (Xu and Crouch 2008). Gene/QTL pyramiding can be achieved through either multiple-parent crossing or complex crossing, backcrossing, and recurrent selection; and marker-assisted pyramiding of multiple QTLs will be a promising approach to enhance the stability of crops under stress (Richardson et al. 2006). The success of marker-assisted gene pyramiding depends on multiple factors, like the number of gene/QTLs involved, the distance between the QTLs, the number of parents involved or required, MTAs, and the relative cost. Currently, several resistant common bean cultivars were developed to improve levels of resistance to anthracnose, angular leaf spot, rust, and BCMV (Ragagnin et al. 2009).

Souza et al. (2014) used a marker-assisted gene-pyramiding approach to develop elite carioca bean lines harboring three different rust resistance genes, which was

only possible because the Rudá recurrent parent has a high-yield performance. Likewise, focusing on anthracnose and Pythium root rot resistance, Kiryowa et al. (2015) pyramided genes in four susceptible market class varieties using SCAR markers. They also demonstrated that higher numbers of selected pyramided genes may indirectly affect yield by reducing the number of seeds per plant. Further, through MAS, Ragagnin et al. (2009) developed pyramided lines resistant to rust, anthracnose, and angular leaf spot. These demonstrated resistance spectra equivalent to those of their respective donor parents, and yield tests showed that these lines were as productive as the best carioca-type common bean cultivar.

1.8.4 Limitations and Prospects of MAS and Marker-Assisted Backcrossing Breeding (MABCB)

MAS is an important tool for supporting plant breeders in crop improvement. It considerably increases the efficiency of breeding, when markers tightly linked to genes of interest are used. Despite its advantages, MAS might not be as successful as expected when QTL introgression is necessary (Kumar et al. 2011), and MAS is not always better or more cost-effective than direct disease resistance (DDS), especially for quantitatively inherited resistance to diseases. Efficient comparison of these two techniques, regarding pyramiding and transfer of CBB resistance into dark red kidney bean, showed that DDS was significantly more effective than MAS (Duncan et al. 2012). Under greenhouse conditions of high disease pressure, DDS produced more resistant breeding lines with greater levels of resistance than MAS. MABCB is considered smart breeding for different reasons. First, it is a nontransgenic biotechnological approach to plant improvement and is not subjected to rules/regulations that restrict its use. Secondly, disease resistance selection without the use of a pathogen is feasible, and off-season screening is possible. Finally, it is suitable for combining multiple sources of disease resistance for distinct pathogens.

MABCB represents a rapid and precise molecular breeding technique that assumes superior individuals can be precisely isolated based on genotypes at particular marker loci. In practice, MAS can be exercised in various ways, for example: the marker-assisted evaluation of breeding material, MABC, pyramiding, early generation selection, and combined MAS (Collard and Mackil 2008). Fortunately, molecular markers have many more applications beyond this scheme. To execute MAS more efficiently, DNA markers must have some key features, like greater reliability, quantity, and quality of DNA required, the ease of technical procedure to assay, a high level of DNA polymorphism, and a low cost of assay designing (Mohler and Singrun 2004). Remarkably, Toenniessen et al. (2003) noted a greater efficacy and accuracy of MAS over conventional plant breeding.

Three different types of MABC used for selection have been reported: foreground selection, recombinant selection, and background selection (Tanksley 1983; Young and Tanksley 1989; Holland 2004). In foreground selection, genotype of markers

linked to a target gene or QTL can be used either in combination with a phenotype or to replace screening for the target gene or QTL, particularly for useful traits that are generally measured through laborious and time-consuming phenotype screening procedures (Hospital and Charcosset 1997). In recombinant selection, backcrossed progenies are selected with the target gene, and recombination events are selected between the target locus and linked flanking markers. The fundamental idea that underlies recombinant selection is to reduce the size of the donor chromosome segment at the target locus (Collard and Mackill 2008). Nevertheless, the marker-assisted backcrossing MAB (Ribaut et al. 2010) method has been the most effective strategy employed to obtain beneficial QTLs from donor parents with a shortened time frame in both foreground and background selection (Kelly 2004; Varshney et al. 2010). Kaeppler (1997) reported that inbred backcrossed lines may facilitate QTL detection, as these *loci* have a greater probability of being identical by descent, and their interaction with other traits is more sharply detected (Teran et al. 2020).

1.9 Actual Context and Future Perspectives

1.9.1 Concerns and Compliances

The future perspective is not only about to promote legumes, including beans cultivation, it involves the effective rebalancing of farming and food, to ensure feasible support for actual and critical challenges, such as sustainable agriculture, food security, agrobiodiversity, conservation, zero pesticide and human health. The environment, people, and procedures through which agricultural and farmed goods are produced, processed, and delivered to customers without jeopardizing the health of the ecosystems and essential cultures that provide food, make up the sustainable food system. The world's population is expected to rise. We will face global problems, the most crucial of which are attaining food security, minimizing the danger of climate change by reducing net greenhouse gas emissions into the atmosphere, and meeting the growing need for energy. Climate change, as well as biotic and abiotic stresses to which agricultural systems will be increasingly exposed, will have severe consequences for world food production.

According www.pulsesincrease.eu there is a huge potential of *Phaseolus sp.* among other legumes to deliver benefits for food security and clean environment, its exploitation is limited, mainly due to the modest breeding investment and limited research activities on some constraint aspects of species cultivation. The genetic potential remains largely unexplored making the marginal return of investment in legume research likely to be much higher than in other species where research has been much more intensive but where crop improvement is now stagnating.

International studies reflect the fact that performance of beans continues to request significant investment in plant breeding and improving cropping systems. There is a

vast amount of leguminous genetic resources (GenRes) that requires evaluation, characterization, conservation to be superior exploited in various industries. According to IPCC report 2019 titled—Climate Change and Land (https://www.ipcc.ch/report/srccl/) the move to new plant-based diets might provide considerable potential for adaptation and mitigation while also providing significant health advantages. At the same time, there is an increased need to make this genetic material and the knowledge about it, visible and accessible to various groups of stakeholders as: farmers, breeders, processors in the food industry, nutrition specialists, technologists, health care actors, gene banks curators, crop specialists, policy makers. Technologies that have as its basic principle the functionality and access to information and genetic material to facilitate the beneficial exploitation in the agricultural and non-agricultural sector need to be developed. Sustainable development of agriculture is the core of agricultural policy in Europe, and common bean research can ensure new value chains, niche markets, scaling-up of plant breeding efforts, quality of life reflected in safety food and clean environment. The context of COVID 19 highlights the need of reconciling our food system with the demands of the earth, as well as responding constructively to genuine desires for healthy, fair, and ecologically sustainable practices. The moisture contents of all the dry legumes are in the range of 9–13% making them favorable for long storage. Food legumes and legume-inclusive agricultural systems can play a significant role by providing various services while adhering to sustainability standards. Featured by high variability, valuable for food, (inter)cropping, potential medicinal effect, highly required by market, *P. vulgaris,* is one important species to be exploited byEU new protein plan and H2020 funded and currently developed projects. Currently the breeding efforts can open significant opportunities to ensure development of new resources featured by improved resilience and superior qualitative traits, aimed to support the competitive shifts to health diets and to implement friendly cultivation technics. To achieve these ambitious goals and to expand food security, the new breeding materials must be efficient when grown under water, temperature, and nitrogen constraints, as well as resistance to pest and disease.

Grain legumes are the most important source of plant protein worldwide, particularly in many African and Latin American regions, although they have several challenges in production, including poor adaptability, pest and disease problems, and inconsistent yield production.

Screening the limits and trends surrounding bean production and commercialization offers background for determining prospective research priorities based on regional and national constraints and needs. Related the strong variability in yields along years more important focus concerning the reliable food supply and income of smallholder farms is needed. Nassary et al. (2020) recommends as valuable specific investigations related intercrop system for a certain altitude, during long periods.

1.9.2 Opportunities and Challenges

Related adaptation for development of sustainable agriculture– some legumes are adaptable to cultivation under unfavorable ecological conditions, nutritious and stress tolerant, possessing characteristics for enhancing the sustainability of different agricultural systems. Modern cropping methods are designed to decrease the need of external inputs and to take use of legumes' ability to fix atmospheric nitrogen, release high-quality organic matter into the soil, and improve soil nutrient circulation and water retention. The aim of these practices and cultivation scheme is to reduce the negative impact of agriculture on environment; Currently, the European Union devotes only 3% of its arable land to protein crops, and imports more than 75% of its plant protein. The main reasons are low yield capacity and lack of breeding efforts for adaptation of legumes to European agro-ecosystems; The low level of European plant protein self-sufficiency is due to the late development and adaptation of protein plants in Europe. Better use of genetic resources represents a precondition to increase sustainability. Common bean (*Phaseolus vulgaris*) was the most extensively grown grain legume in Europe until around 1970. Field pea and soybean became the most widely grown grain legumes when governmental support for soybean and protein feed crops was introduced in the 1970s. Field peas and faba beans are the most common pulses, while lentils and chickpeas are only cultivated in limited areas.

Pea is the most widely grown grain legume in Europe, but it suffers from poor standing ability, poor ground coverage, and low competitive ability against weeds, along with relatively low protein (20%–24%) and, on many soils, low productivity. Faba bean is the second in area, the first in yield per hectare, and on account of its higher protein content (28–32%), the highest in protein yield, but is adapted to heavy or clay-rich soils and too sensitive to water deficit on sandy soils. Lentil, chickpea, and common bean all have protein contents in the same range as that of pea and have relatively low yields, but high values as they are primarily food rather than feed crops. Since 2013, production in the EU has nearly tripled, reaching 6 million t (2.6 million ha) in 2018.

Thanks to their capacity to fix nitrogen in soils by synergic relationships with *Rhizobia* and mycorrhizal fungi, legumes help reduce the need for fertilisers and avoid economic inputs and environmental impacts. The quantity of nitrogen fixed by legumes is influenced by environmental factors such as temperature and water availability, in addition to species and cultivar. This nitrogen is used by the plant to make protein, which is then made available to humans. Reduced insect and weed incidence, as well as better soil quality, are further advantages of legumes that should not be ignored. To cover the increasing amounts of nitrogen requirements during development and filling, pods attract nitrogen from the nodules. If the nodules cannot cover their N requirements, pods attract nitrogen from older leaves, thereby reducing the photosynthetic capacity of the plants and determining rapidity of ripening. Therefore, the selection of rhizobia strains with increased nodulation capacity may improve N

availability to pods, thereby increasing pod size, which is an important quality characteristic. Selection of efficient bacteria requires specific selection processes based on efficiency and competitiveness for nodulation of the associations. In agriculture, salinity is a widespread and severe environmental stressor that is substantially increased by irrigation. Furthermore, incorrect fertilization methods contribute to salt accumulation in the roots zone of plants.

Under these conditions, the usage of commercial inoculants containing arbuscular mycorrhizal fungus is rapidly increasing, and it is being praised as an environmentally benign technique that helps to mitigate the detrimental impacts of soil irrigation water salinity. Intercropping is common in low-input, low-yield farming methods in underdeveloped countries. Despite several well-known benefits of intercropping, such as improved pest control, competitive yields with lower inputs, pollution mitigation, reduced fertilizer-N use, increased utilization efficiency of available nutrients and water, and more stable aggregate food or forage yields per unit area, intercropping is not widely used in modern agriculture due to a number of constraints, like the demand for a single and uniform product, as well as the appropriateness for mechanization or the use of additional inputs. As a result, optimizing intercropping systems is required to improve resource efficiency and crop output while also increasing numerous ecosystem services.

The possibility of intercropping in sustainable productions and grain legumes that can fix nitrogen through biological mechanisms have been the focus of current study. Legumes (top 10 most frequently used intercrop species, seven are legumes) can contribute up to 15% of the N in an intercropped cereal, thus increasing biomass production and carry-over effects, reducing synthetic mineral N-fertilizer use, and mitigating N_2O fluxes.

When maize and beans are intercropped, their yields are generally lower than those of maize or beans grown in monoculture. Studies have found that maize yielded 5.3 t ha^{-1} when monocropped, 5.2 t ha^{-1} when intercropped with bush beans, and 3.7 t ha^{-1} when intercropped with climbing beans. Maize-legume rotations help to keep soil fertilityCereal–legume intercrops can be used for forage or grain depending on growing conditions and farm management and using them for whole-crop silage is a way of boosting the forage protein content of livestock diets. The cereals are generally better than legumes at taking up mineral N. Legume root exudates released phosphate and a variety of cation species, whereas cereal roots released other minerals, resulting in higher P absorption in cereals and Fe and Zn uptake in legumes when compared to single crops.

In systems where nitrogen fertilizer is used rarely or not at all, cereal–legume combinations outperform pure cereals. Chemical weed control is difficult or impossible in intercrops, as few herbicides are tolerated by both a cereal and a legume. Intercroppinggrain legumes and cereals has demonstrated multiple agronomic and environmental benefits. Intercropping, in comparison to grain legume single crops, lowers weed density, contributes to better and/or more stable combined grain yields, reduces the severity of pest and disease issues in both the legume and cereal components, and increases biodiversity to assist pollinating insects (see LEGATO project "LEGumes for the Agriculture of Tomorrow", funded by the European Union under

the FP7 Programme, http://www.legato-project.net/). Grain legumes are poor weed suppressors, however combining species in the same cropping system might be a viable method to increase the crop's capacity to control weeds. Grain legumes substantially decreased emission factors, implying that legume-fixed nitrogen is a less emissive type of nitrogen input to the soil than fertilizer nitrogen. Nevertheless, it is important to highlight that the influence of legumes in reducing GHG depends also on the management of agro-ecosystems in which they are included. Direct reciprocal advantages in cereal-legumes intercropping entail below-ground mechanisms in which cereals improve Fe and Zn bioavailability to associate legumes while benefiting from legume-fixed N. As a result, crops following legumes have higher yields, such as wheat, maize, or rapeseed, which can be up to 10% higher than crops following cereals. Higher yields are therefore observed for crops following legumes e.g., yields of wheat, maize or rapeseed can be up by 10% compared to following a cereal. Following a legume improves also the quality of cereals (e.g., increased protein content or fewer mycotoxins contamination). The inclusion of grain legumes into cropping cycles continues to raise concerns. Cropping systems that include legume crops in farm rotations must be supported by optimal crop management methods (e.g., amount and sequencing of nitrogen fertilization, soil management, weeding, irrigation), which often differ from what farmers are used to.

Ensuring agrobiodiversity and conservation–The Common Agricultural Policy (CAP) in Europe has pushed for agricultural intensification, encouraging the simplicity and specialization of agroecosystems by reducing landscape variation, increasing chemical usage per unit area, and abandoning less productive regions. Herbicide use or monocultures, for example, are high-input agricultural methods that directly impact biodiversity and may disrupt pest management services. Over the last decades, numerous research articles and discussions have focused on the loss of agricultural genetic diversity across farmlands throughout the world, as well as the resulting loss of resistance to climatic, economic, and social severe events. In a number of situations, a lack of crop diversification has resulted in significant output losses. Crop and crop variety diversification is critical for delivering the advantages of agrobiodiversity.

Need for improvement of food legume genetic resources- To date, exploitation of genetic resources in crop breeding is limited in comparison to availability of materials, and the potential impact of their use is far from optimal (i.e., lack of comprehensive information regarding passport data and descriptors useful for users, accession heterogeneity, unharmonized data), which also affects ability to attract funds for genetic-resources conservation. These issues are more critical in food legumes, as breeding investment and research activities remain modest. Efficient genetic-resources management is required to attract further private and public investment to improve food legumes breeding. From this perspective, the availability and access to well-described and well-managed genetic-resource collections of food legume species that capture the full diversity range will be paramount to advance legume crops and to reach a competitive level in the EU regarding agronomic performance and sustainability. Indeed, without correct handling of EU legume genetic resources, the European Commission's goal of achieving the nine CAP objectives

(i.e., economic, environmental, climatic and socio-economic, including healthier diets) will be unattainable. In this context, large scale projects such as INCREASE—Intelligent Collections of Food Legumes Genetic Resources for European Agrofood Systems, recently funded through the European Union's Horizon 2020 research and innovation program (https://www.pulsesincrease.eu/), aims to improve the sustainable use of GenRes by developing efficient and effective conservation tools to promote agrobiodiversity and its use. According to INCREASE, the actual utilization of grain legumes GenRes is limited in comparison to the availability of materials and the potential impact of their use, due to several concurrent factors: (*a*) *genetic structure of accessions* - in most cases, accessions have unknown genetic structure and are heterogeneous, which impedes the projection of the phenotypic information to the genotype and vice versa. (*b*) *limited information availability on GenRes*: large numbers of accessions have only minimal, if any, information regarding biological status and geographic origin; information regarding traits of interest for breeders and users is very low and mostly limited to morphological descriptors; (*c*) *limited access to available information* (*) the heterogeneous nature and non-standardised way of data collection and integration causes that a huge amount of information is heavily under-used; (**) databases are centralized and not designed to integrate data obtained by external users strongly limiting the access to available information; (***) the available information is not easily accessible to users due to unfriendly searching and visualization tools. Accession-based collections are built and maintained, with each accession often including a mix of genotypes that reflect a population. The conservation of the population represents substantial challenges that arise from genetic drift and/or selection, which are difficult to fully address in conventional conservation management, and from the lack of knowledge of their diversity.

Beans a bridge between food and health **-** Diets throughout the world have changed dramatically; in most of the countries studied, more calories are consumed per person, and the percentage of fat and animal protein taken has grown greatly. Diet is nowadays considered as crucial not just for nutrition, but also for disease prevention and treatment, particularly when diseases are caused by insufficient, excessive, or unbalanced food consumption. One of the most controversial subjects of discussion is the establishment of an optimum human diet. Grain legumesspeciesare featured by superior quantity of protein comparing with other plant foods and have twice the dietary protein content of cereal grains, strongly having perspective to exploited against malnutrition and generally in food sector; The content of bioactive substances can be altered by genetic improvement of nutritional value. Recent investigations suggest that grain legumes may contribute to human health and wellbeing, mostly through prevention of chronic diseases like coronary heart disease, hypertension, cancer, diabetes, and obesity. Due to their satiety value, legumes contribute to regulate body weight and lower the risk of cardiovascular disease and several cancers. The influence of micronutrients (primarily folic acid and magnesium) and high fiber content, condensed tannins, phytoestrogens, and non-essential amino acids in common beans contributes to the prevention and/or treatment of degenerative-chronic diseases such as obesity, diabetes, cancer, and cardiovascular diseases. Common beans are a good

source of aromatic amino acids, lysine, leucine and isoleucine, but deficient in sulfur amino acids (methionine and cysteine), valine, tryptophan and threonine.

Pulses represent an important source of protein for vegetarians, are low glycemic index food and recognized as food choice with significant potential health benefits. They are excellent foods for people managing their diabetes, heart disease or celiac disease, and additionally can help people concerned with weight control. To improve the nutrition of many developing countries, or to combat the incidence of various chronic diseases worldwide, food technologists have developed products based on pulses, adding value thereby contributing to increase in the consumption of legumes. Legumes have appreciable quantity of all the essential amino acids excluding sulphur containing amino acids, which can be balanced to combine with cereals in daily intake. Moreover, legumes seeds also include calcium, magnesium, potassium, phosphorus, and iron. Bioavailability of nutrients can be increased by soaking, sprouting and fermentation. Grain legumes contain 20–45% protein compared with 7–17% in cereals. The protein content ranges from 20 to 25% in common bean (*P. vulgaris*). On the other hand, legumes are incomplete proteins (except soy) because they contain relatively low quantities of the essential sulphur containing amino acids cystine, methionine and cysteine (which are found in higher quantity in grains).

However, grains contain relatively low quantities of lysine, whereas legumes contain appreciable quantity. Pods and immature seeds of legumes contain less proteins than dry seeds of the same species. The nutritional value of legume vegetables as protein sources is determined by their amino acid composition and protein digestibility, as well as their protein amount. Adequate dietary fiber is vital for proper working of the gut, which is related to reduce risk of several chronic diseases including certain cancers, heart disease and diabetes. Fiber comprises pectin, mucilage, cellulose, gum, hemicelluloses and lignin. Most of the legume grains which are consumed as pulses by humans, their fiber content ranges from 0.9 to 5.3%. Legumes are mainly rich in resistant starch (RS), have low glycaemic index carbohydrates. The oligosaccharides (mainly raffinose and resistant starch) and fiber pass through the stomach and small intestine in the undigested form until they reach the colon, where they act as food (prebiotics) for the probiotic or beneficial bacteria which resides there. This bacterial fermentation leads to the development of short-chain fatty acids, such as butyrate, which possibly will improve colon health through promoting a healthier gut micro biome and reducing colon cancer risk. They also can help in weight reduction due to its satiety value. In addition, they are capable to help in moderating blood sugar levels after meals and improve insulin sensitivity.

Commonly consumed legumes having carbohydrate content in the range of 20.9–60.9%. In legume seeds, starch is the main source of accessible carbohydrate and most plentiful 22–45% along with 1.8–18% oligosaccharides and 4.3–25% dietary fiber. Legumes are excellent source of iron, calcium, zinc, selenium, magnesium, phosphorus, copper and potassium. Cereals grains generally supply the higher energy and make up the volume of diets. As sources of micronutrients legumes are superior to cereals. Most legumes, including common beans are consumed whole, resulting in conserving their mineral contents. Micronutrient deficiencies have become more common, even in developed countries. Legumes are superior source of vitamin

B-complex but are a poor source of vitamin C and fat-soluble vitamins. Legumes are normally low in fat and have no cholesterol, with soybeans and peanuts exception. Mono and poly unsaturated fatty acids decrease the possibility of coronary heart diseases. Legumes have anti-nutritional factors which affect its nutritional quality. Anti-nutritional factors can reduce palatability, protein digestibility and bioavailability of nutrients. Phytic acid, phenols, and tannins, which were once thought to be antinutritional, are now considered to be potential antioxidants with health-promoting properties. Phytochemicals reduce the digestion and absorption of nutrients or interfere with their action. The bioactive phytochemicals including enzyme inhibitors are mainly represented as phytoestrogens, oligosaccharides, phytosterols, phytates, saponins, flavanoids and phenolic acids.

Grain legumes are the main sources of lectins in human food. Beans (most species, including *P. vulgaris*) appear to be a significant source of lectins. Lectins found in certain pulses can make food proteins less digestible and biologically valuable. Lectins, on the other hand, may be beneficial by improving gastrointestinal function, decreasing tumor development, and reducing obesity. The importance of phenolic compounds has progressively been acknowledged, and various studies have recently shown that phenolic compounds have several health advantages and are essential in human nutrition. There have been reports of strong links between phenolic contents and antioxidant activity. The highest antioxidant capacity is found in pulses with the highest overall phenolic content (lentil, red kidney, and black bean). Many pulses, such as lupin, lentil, and chickpea, as well as different beans and peas, have been shown to contain saponins. Saponins may have hypocholesterolemic, anticarcinogenic, and immune-stimulatory effects, according to new research. Since excessive generation of free radicals/reactive oxygen species (ROS) and lipid peroxidation are commonly thought to be implicated in the etiology of many illnesses such as cardiovascular diseases, cancer, and autoimmunity, the antioxidant capabilities of food have been intensively investigated.

New innovative products– the market for pulses for food in the EU is benefitting from innovations in pre-cooking processes, inclusion of pulses in prepared convenience foods and the development of new pulses such as ‘edamame’. Extruded beans, which have a high protein content, might be utilized as a basic material for the production of high protein snack bars since their flavor is sufficiently neutral, allowing them to be used for both salt and sweet snacks. An added value can be given by adding functional supplements such as hemp seeds, goji berries, ginger, and others (see EUROLEGUME project, “Enhancing of legumes growing in Europe through sustainable cropping for protein supply for food and feed”, funded by the European Union under the FP7 Programme, http://www.eurolegume.eu). As a result, including bean flour into cereal foods can enhance protein, soluble fiber, vitamin, and mineral content.

Using selected legume genotypes, a variety of innovative products were developed, including pea and bean immature seeds with extended shelf life, pesto sauce made from legume seeds, ready-to-eat pulse spreads, extruded snacks made from dry pea and bean seeds, and protein and fiber rich legume bars in a variety of flavors (EUROLEGUME).

In 2016, the new Bean Beer was introduced as a beer made with 40% whole faba beans and 60% malted barley. The beer is marketed as a sustainable drink made as it is made from a crop that contributes to more sustainable farming practices. There are new opportunities of using legumes for food products of improved nutritional value.

Another outstanding challenge is the strong need to ensure the availability of education and training at all levels to build capacity, infrastructure, and networks to establish and maintain credibility and professionalism. To ensure the functionality and competitiveness friendly cultivation there is a need for all stakeholders, namely, government agencies, non-governmental organizations, consumers, and farmers' organizations, to work together.

1.9.3 Potential for Expansion

Industrialized agriculture has expanded during the past few decades, and along benefits a lot of negative input it has been brought into environment. Fortunately, an important opportunity also exists for the expansion of friendly environmental areas. There are many areas in that feature significant crop genetic diversity, where farmers still practice traditional agriculture and cultivate local varieties that have been selected over the course of many generations. Various programs and research projects have organized collection missions whose purposes is to collect genetic material and knowledge related to conservation techniques and cultivation methods, with the goal of to be valorized in pre-breeding and breeding. There is a strong need to detect and use the specific traits related to organoleptic qualities, and yield capacity, tolerance, and resistance to biotic and abiotic stress.

One challenge facing organic production systems all over the EU is the urgent need to provide climate-resilient cultivars. Currently, one going European project BRESOV ("Breeding for Resilient, Efficient and Sustainable Organic Vegetable Production ") started from the need to increase the plants' tolerance to biotic and abiotic stresses and adapt the varieties to the specific requirements of and low-input production processes has set out to improve the competitiveness of three important vegetable crops one being snap bean in an organic and sustainable environment. The BRESOV project aims to create a pipeline for crop improvement that will accelerate the production of high-quality organic seeds for breeders and farmers around the world. The pressure of climate changes requires the urgent need to provide climate-resilient cultivars technics and methods addressed to organic and conventional vegetable production systems and farmer's access to safe and quality seeds for resilient varieties and friendly technics. These new resources will benefit growers, seed industry, providing much needed security both under current and future scenarios of climate change.

The exploit of the genetic variation of legumes species for enhanced productivity, by exploiting up-to-date knowledge of genome structure and function for use in different directions as conservation, human health, sustainable agriculture can ensure long term benefits for human and environment.

Beans represent a valuable source of food proteins, and their exploitation is expected to increase in relation of a growing world's food need. The actual context of the need for available, healthy, long self-life food, new opportunities and challenges for the agriculture and food sector open. The value chain needs a strong improvement with new varieties with higher adaptation to different environments, better yield and improved qualities with a particular concern in the development of new products with high organoleptic and nutritional value. The availability of novel varieties will facilitate the adoption of food legumes in the agroecosystem improving the agrobiodiversity with all its related positive consequences associated to the inclusion of legumes in the cropping systems (e.g., sustainability, food security, economic returns, stable farming systems, increase of soil fertility, diversify products, improve human nutrition, etc.).

For the sustainable use of genetic resources, a coordinated, interdisciplinary, and multi-sectorial effort is needed to exploit the recent scientific and technological ground-breaking advances. Grain legumes should be reintroduced into crop rotations in the future, based on their favorable impact on production and quality attributes of following crops.

The market for meat and dairy alternatives is particularly promising, with annual growth rates of 14% and 11%, respectively. This implies huge opportunities for innovation based on added value to primary production. Strategies and plans to improve nutritional and quality traits need to be implemented to provide affordable supply for all citizens. To build these new capacities and innovative products, links to local, regional production and food tradition, which have as focus the consumer preference had to be valorized. These challenges meet citizens' needs and preferences (e.g. changing dietary habits), regarding impact on health, environment and climate change mitigation. Alternative plant proteins for food are demanded. The EU has developed a new protein plan, and its implementation will be largely based on traditional and innovative uses of food legumes and reflects the high interest of the food sector for development of products to meet consumer requests for healthful diets. In several EU states, human plant protein consumption is increasing.

Moreover, most of legume species can establish symbiotic association with nitrogen fixing bacteria, collectively known as rhizobia. Nitrogen fixation underlies the high protein content of legume seeds, and it is also of immense economic and ecologic importance, because it returns vital reduced nitrogen to the soil, thereby enhancing (agro)ecosystem productivity and sustainability. Historically, legumes were a primary source of agricultural nitrogen because they were grown in rotation with cereals. In most modern intensive agricultural systems, however, including those of Europe and North America, nitrogen fertilizer originates from industrial processes (Haber Bosch) that require immense quantities of fossil fuel to reduce N_2 to NH_4. Therefore, production of industrial fertilizers contributes ~ 3% of global CO_2 and is a primary source of pollutant NO_2. Moreover, runoff from fertilizer is among the world's most serious environmental pollutants, causing eutrophication of marine systems. Therefore, exploiting legume GenRes to improve the symbiosis between crop legumes and their rhizobia could have major impact on sustainable agriculture and the world's economic, social and environmental health.

1.10 Treaties and Conventions. Disclosure of Sources of Genetic Resources. Access and Benefit Sharing

Food safety, seed security, diversity, and clean environment are important keys, considered priority "0" at planetary level in researchers and politicians' agenda, aimed to design new strategies for the benefit of current and future generations. In this context, plant genetic resources for food and agriculture (PGRFA) are essential for achieving global food security and for sustainable agricultural development in the context of poverty mitigation and climate change. PGRFA are crucial to adapting plants to a changing and more complex environment, but their variability in current breeding, farming and forest management remains largely underused. Conservation initiatives (in-situ, ex-situ) are aimed at capturing, maintaining and making a large share of these global assets available. Access to resources, however, is also limited by the nature of the content and the knowledge provide by the different conservation sites. With growing concerns about biodiversityand genetic loss, joint efforts to extend and enhance the protection and use of PGRFA in farming and forestry has led to the development during the last few decades of numerous international instruments, treaties and conventions to ensure the efficient management of PGRFA. The Convention on Biological Diversity (CBD), the Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from the Utilization (hereinafter referred to as the Nagoya Protocol), the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) and various types of intellectual property rights are some examples of these.

The CBD is the first global agreement aimed on conservation and use of biological diversity to recognise the jurisdiction of states over their genetic resources in relation to their conservation and sustainable use, the traditional knowledge of the indigenous and local communities, and the allocation to these communities of the benefits derived from their use. The CBD, as an international treaty, recognizes a shared problem, establishes overarching aims and policies, as well as general commitments, and arranges technical and financial cooperation.

- National actions, the countries have a major share of the responsibility for accomplishing their objectives. Conservation and sustainable use of each country's biological diversity can be achieved in various ways. The major method of conservation, "in-situ" conservation, focuses on preserving genes, species, and ecosystems in their native habitats, such as through establishing protected areas, restoring damaged ecosystems, and enacting legislation to preserve endangered species. To save species, "ex-situ" conservationists employ gene banks. In the years and decades ahead, promoting the sustainable use of biodiversity will become more important for conserving biodiversity.
- International action, the Convention's success depends on the combined efforts of the world's nations. Individual nations are responsible for implementing the Convention, and compliance will be largely based on informed self-interest and peer pressure from other countries, as well as public opinion (text from the

document Sustaining life on Earth How the Convention on Biological Diversity promotes nature and human well-being by, Secretariat of the Convention on Biological Diversity April 2000).

The Nagoya Protocol, approved in 2010, considerably expands and fleshes out the broad framework provided in the CBD for access to genetic resources and the fair and equitable sharing of benefits arising from their use (access and benefit sharing). The ITPGRFA, adopted in 2001, established an international legal framework for the conservation and sustainable use of genetic resources for food and agriculture, as well as the equal and equitable sharing of benefits arising from their use, in accordance with the CBD and with the UN's Food and Agriculture Organization. The Nagoya Protocol's application and the ITPGRFA's application are meant to be complimentary. The Nagoya Protocol does not apply for the Parties to the ITPGRFA in respect of the PGRFA covered by and for the purpose of the Treaty. However, the Nagoya Protocol and the ITPGRFA are based on two separate models of structures for access and profit sharing. The Nagoya Protocol establishes that, in accordance with national legislation, access to genetic resources and to its associated traditional knowledge for their utilization is subject to obtaining the prior informed consent (PIC) from the provider and to the establishment of mutually agreed terms (MAT), which are to be agreed between the user and the provider. The ITPRFA establishes a "multilateral access and benefit-sharing system" whereby countries agree to practically pool and offer facilitated access to "all PGRFAs listed in Annex I of the Treaty that are under the management and control of the Contracting Parties and in the public domain". The Treaty's Annex I encompass 64 crops and forages that have been selected according to food protection criteria. Under the terms and conditions of the Standard Material Transfer Agreement (SMTA), such facilitated access under the ITPGRFA is given where the intended use of the genetic resource is its conservation and sustainable use for research, breeding and training for food and agriculture. Common bean is included in the crops mentioned in the ITPGRFA Annex I. Access to common bean genetic resources by any legal or private person from any ITPGRFA Contracting Party should therefore be facilitated under the conditions laid down in the SMTA, given that the intended uses are those cover by the ITPGRFA. The Treaty has made legal provisions to facilitate access and benefit sharing and addressed the germplasm utilization issues, which are important for crop improvement. In this context, there is a need to harness the designated germplasm in the gene banks, which includes many wild relatives (CWR) of food legumes. Without any hassle of fresh collecting, the wild relatives and other in-trust accessions held ex situ in gene banks can be used in research and varietal development programs. Molecular and classical breeding approaches can be supplemented to create diversity as well as new plant types suitable for use in different cropping systems and situations. The Treaty encourages the establishment and preservation of various farming systems while also maximizing crop usage and breeding.

Since January 2007, the Multilateral System of Access and Benefit-Sharing became live and the Secretariat created a set of SMTA users' optional information technology tools. In 2009, the Secretariat, in partnership with CIRAD, published the

first edition of Gene-IT, a user-friendly standalone software program for filling out and generating SMTAs. To make SMTA providers' reporting responsibilities easier, the Secretariat created and released an information system in November 2010 that permitted online reporting at the accession level for the specific crops mentioned in Annex 1 of the Treaty. The experience of the Secretariat of the International Treaty has allowed for modifications since then.

A set of new measurements is under implementation in frame of Green Deal. The recently released "Farm to Fork Strategy", which aims to design a strong food system capable of ensuring access to a sufficient supply of affordable products and services for all citizens, brings together international consortia to test and demonstrate systemic innovations, including leveraging legumes' multiple benefits.

1.10.1 Farmers Rights

Apart from theInternational Treatyitself—the Convention on Biological Diversity (CBD), the Agreement on Trade-related Aspects of Intellectual Property Rights (TRIPS) of the World Trade Organization (WTO), the Convention of the Union for the Protection of New Varieties of Plants (UPOV) and World Intellectual Property Organization (WIPO) of the United Nations (UN) are among the most important international agreements. These international agreements are interlinked, and they interact in various ways about Farmers' Rights, to ensure recognizing of paramount contribution of farmers to the diversity of crops that feed the world. Farmer rights are referenced also by establishing a global network with access to plant genetic materials for farmers, plant breeders and scientists.

TRIPS is an international legal agreement that all WTO members have signed. It establishes basic standards for national governments to regulate different forms of intellectual property rights (IPR) that affect citienzens of other WTO member nations. The TRIPS agreement, in particular, calls for stronger protection in areas that were previously unprotected by formal IPRs in many nations, such as genetic resources (including plant varieties). Consequently, countries around the world are gradually adopting plant variety protection legislation in line with the rules laid down by the International Convention for the Protection of New Varieties of Plants (hereinafter referred as the UPOV Convention). The UPOV Convention is a sui generis form of protection of intellectual property, specifically designed to reflect the specific characteristics of the breeding, cultivation and use of new plant varieties. The Convention was adopted the first time in 1961, and was subsequently revised in 1972, 1978 and 1991. As of February 2020, this organization had 76 countries (including the African Intellectual Property Organization and the European Union) as members (www.upov.int). UPOV's objective is to establish and support an effective system for plant variety protection, with the goal of encouraging the production of novel plant varieties for the benefit of society. The breeder's right is guaranteed for a period of not less than 20 years from the date of grant or, in the case of trees and vines, for a period of not less than 25 years. Accordingly, a breeder's authorisation is necessary for the

use of the reproduction or propagation material. However, the right of the breeder under the UPOV Convention does not apply to actions taken out privately and for non-commercial reasons, to actions taken for experimental purposes and to actions carried out for the purpose of breeding other varieties and to the exploitation of those new varieties, given that the new variety is not necessarily a variety derived from another protected variety. As of January 2021, the UPOV PLUTO database includes 12,343 varieties of genus *Phaseolus and* provided by 57 countries (last accessed in January 2021—available at http://www.upov.int/pluto/en/).

1.10.2 Participatory Breeding

International, breeding programs are often aimed at producing high-input commercial farming plant varieties that perform well in standardized environments. As a result, these varieties are typically not sufficient for the non-uniform conditions typical of marginal areas or for those farmers who are unable to buy additional inputs. In this context, participatory plant breeding and participatory variety selection will be crucial to strengthen the least productive common bean systems and to provide varieties that respond well to agro-ecological management under an integral ecology approach. Participatory plant breeding and participatory variety selection are methods in which farmers and officially qualified breeders work together during different phases of the breeding process, often locating breeding plots in the fields of farmers rather than in agricultural research stations and selecting agronomic and quality features adapted to the particular requirements of farmers. A number of successful implementations of this approach have been documented for common bean in Central Africa, Kenya, Rwanda, Uganda, Ethiopia, and in Kashmir.

With the aim to preserve, rebuild, revitalize, reinforce and develop local seed systems, with an emphasis on local varieties, community level seed-saving programs have been also developed for over 30 years. Community seed banks are run by local organizations that hold collections of seed that are maintained and administered by communities in a central facility or in a structure that is shared among a range of individuals. Community seed banks play different functions in the community such as preserving seeds, providing access to seeds for community members, and generating a degree of food security and food sovereignty, while at the same time contributing to the implementation of farmers' rights through the recognition of farmers' knowledge of local biodiversity, their participation in decision-making for its conservation and benefit sharing.

An important tool for sharing knowledge and plant genetic resources for sustainable use in breeding can be the **European Cooperative Programme for Plant Genetic Resources (ECPGR), EURISCO cathalog and AEGIS system**. This is a multi-country initiative aimed at guaranteeing the long-term conservation of plant genetic resources and making their use more accessible throughout Europe. In frame of this Program is function a working group dedicated to grain legumes species. In Europe stakeholders collaborate to conserve ex situ and in situ PGRFA, provide

access and increase sustainable use with the aim (i) to efficiently conserving and providing access to unique germplasm in Europe through AEGIS and the European Collection; (ii) to offer through the EURISCO catalogue passport and phenotypic information of actively preserved European PGRFA; (iii) to improve in situ conservation and use of crop wild relatives; (iv) to promote on-farm conservation and management of the diversity in European PGRFA; (v) to promote use of PGRFA.

1.10.3 Conclusion

It is evident that common bean improvement is an ongoing process and there is still great potential to exploit the genomic information and genetic diversity to maintain continued yield gains and to face agricultural challenges, such as climate change and food security. However, the use of genetic resources in common bean breeding to date is minimal relative to the availability of materials, and the possible effect of their use is far from optimal (i.e. lack of detailed knowledge on passport data and user-useful descriptors, accession heterogeneity, non-harmonized data). In this context, large scale projects such as INCREASE (https://www.pulsesincrease.eu/), aims to improve genetic resources use by developing efficient and effective conservation strategies to promote agrobiodiversity and its use.

Finally, it is also important to recognize the current advances in agro-biotechnology in molecular markers, functional genomics, mutagenesis, tissue culture, genetic engineering and even deep phenotyping approaches and sophisticated informatics tools, when designing new breeding programs aims to obtain new varieties with broad resistance to varied biotic and abiotic stresses. This is reflected in efforts already underway within large scale projects such as the BEAN_ADAPT Project (funded through the second ERA-CAPS call; ERA-NET for Coordinating Action in Plant Sciences), BRESOV H2020 funded project. The projects areusinga multidisciplinary approach (i.e., genomics, transcriptomics, metabolomics, plant physiology, population/quantitative genetics and biochemistry) to expand the genetic basis of phenotypic adaptation in *P. vulgaris* and its sister species *P. coccineus*across Europe and outside their origin centers.

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